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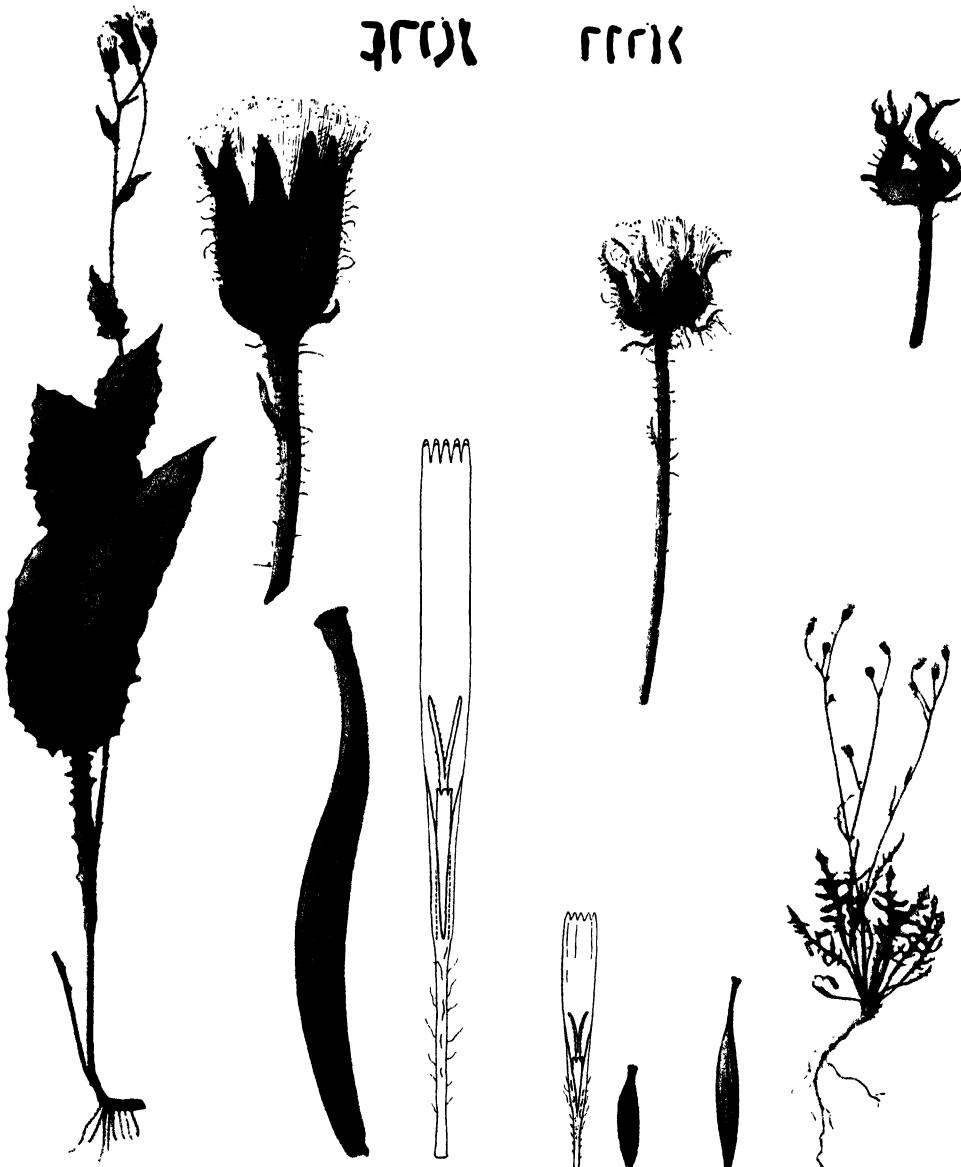
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LEE BONAR
A. S. FOSTER
H. L. MASON





Crepis sibirica (left), the most primitive, and *C. suberostris* (right), the most advanced species in the genus having 5 pairs of chromosomes. *C. sibirica* is a widespread perennial species of northern Eurasia; it is a typical cryptophyte with a rhizome. (Note the large lyrate leaves, the few large flower heads, especially the involucre with many large bracts, which remain unchanged at maturity, and the comparatively large size of the individual floret and the columnar achene.) *C. suberostris* is a polymorphic annual species of Algeria. The plant shown above is subsp. *typica* which occurs only in a small area in the littoral sand dunes; whereas subsp. *arenosa*, which is represented above by the finely beaked achene, occurs more widely in the arid uplands. (Note the branching taproot, the smaller dissected leaves, the numerous small heads, the involucres with few small bracts and with basal thickening at maturity, the comparatively small floret and achene, and the presence of a beak on the achene.) All to the same scales.

THE GENUS CREPIS

PART ONE

*The Taxonomy, Phylogeny, Distribution,
and Evolution of Crepis*

BY

ERNEST BROWN BABCOCK

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Part One

THE TAXONOMY, PHYLOGENY, DISTRIBUTION,
AND EVOLUTION OF CREPIS

Part One of this work embraces pages i–xii + 1–198, in which are included frontispiece, plate 1, text figures 1 to 11 and A–D, and tables 1 to 12.

Part Two (University of California Publications in Botany, Volume 22)
subtitled

Systematic Treatment

embraces pages i–x + 199–1030, in which are included plates 2 to 36, text figures 12 to 305, and tables 13 to 19. The treatment of the 27 sections, giving detailed data on the 196 species of the genus, is introduced by subdivisions entitled general plan, descriptions, abbreviations and citations, history, diagnosis, and description of the genus, diagnosis of the sections, and key to the sections. Following the sections are named hybrids, species not sufficiently known, excluded names, and indexes.

CHAPTER 1

HISTORY OF THE INVESTIGATIONS, WITH RESULTS AND CONCLUSIONS OF SIGNIFICANCE FOR SYSTEMATICS

EARLIEST STUDIES, 1915-1922

THE INVESTIGATIONS which led to the writing of this monograph had their inception in 1915 when the published reports of Rosenberg (1909a) and Digby (1914) that *Crepis capillaris* has 3 pairs of chromosomes in its somatic cells, and of Juel (1905) and Rosenberg (1909a) that *C. tectorum* has 4 pairs of somatic chromosomes, were brought to the attention of the author. The importance of the low number of chromosomes in *Drosophila melanogaster* in expediting the research which led to the epoch-making discoveries of Morgan (1915) suggested the possible value of these species of *Crepis* for genetic investigations. Seeds of the two species mentioned above were obtained from several botanic gardens and from the wild; and extensive garden cultures were grown in 1917 and 1918 from which many selections were made for the study of variable characters. At the same time, attempts were made to produce hybrids between these two species. The results of these early studies are mentioned below under genetic research.

In 1918 these *Crepis* investigations were recognized by the California Agricultural Experiment Station as a major project of the Division of Genetics. Since that time, funds have been allocated annually for the maintenance of the project. These funds, together with other funds mentioned below under acknowledgments, have made possible the continuity of research which has resulted in many publications, some of which are listed among the references at the end of this volume, and in the preparation and publication of this monograph. The first mention of the *Crepis* work in the annual reports of the California Agricultural Experiment Station is found in the report for the year ending June 30, 1920 (cf. Babcock, 1920-1932).

This continuous support of fundamental research on a group of noneconomic plants throughout a period of twenty-five years by an agricultural institution reveals a far-sighted policy on the part of the administration of the California Agricultural Experiment Station. It is the hope of the author that the results of these investigations, as summarized by this monograph, will be found to justify such a policy.

Although the genus *Crepis* includes no cultivated crop plant, some of the species are of value for one purpose or another. Many species of *Crepis* are valuable as wild forage for cattle and sheep. This is certainly true of the native western American *Crepis* and it holds good for several species in the Mediterranean region. The fact that *C. divaricata* of Madeira is now almost extinct is undoubtedly due to its use as a forage plant for goats and pigs. Furthermore, some of the Old World species are used by the country people as green salads and it is not unlikely that some of them could be developed into useful cultivated salad plants. In *C. palaestina*, for example, cultivated strains exhibited wide differences in leaf size, amount of pubescence, and degree of bitterness when chewed, and some of these strains seemed fairly promising. As an ornamental, *Crepis rubra* has long been grown in Old World flower gardens. Another pink-flowered species, *C. incana*, is a desirable plant for rockeries. Some of the perennial and biennial species have showy yellow flowers, and one of these, *C. chondrilloides*, is interesting because of its remarkable laciniate leaves. At least one species seems to be of some importance as a plant producing medicinal

poison. *Crepis latialis* of Italy is reported to be extremely poisonous and to be of value in certain heart ailments (see Part II, p. 446). Finally, two common Old World weeds, *Crepis capillaris* (*C. virens*) and *C. vesicaria* subsp. *taraxacifolia* (*C. taraxacifolia*), as well as the rare alpine species, *C. incana*, have recently been found to yield a substance which inhibits the growth of *Staphylococcus aureus* (Osborn, 1943). The evidence reported by Osborn has shown that antibacterial substances are present in very many green plants. The investigation of *C. vesicaria taraxacifolia* by Heatley (1944) shows that the substance "crepin" is antibiotic, since human leucocytes became sluggish but survived for two hours in a solution of 1 in 4,500,000. Yet even at 1 in 4,500, the strongest solution tested, a few cells were alive after two hours, a rather remarkable fact. Crepin also inhibits the growth of *Streptococcus pyogenes* and several other bacteria. It does not occur in free form but as an antibiotically inactive precursor. The agent, presumably an enzyme which activates the precursor, appeared to be confined to the yellow ligules of the florets and, to a much smaller extent, to the roots; whereas the substrate from which crepin is liberated occurs, except for the stem and leaves, in most parts of the plant. Crepin crystallizes from alcoholic solutions in three forms. The yield is small, rarely exceeding 100 milligrams of pure crystals per kilogram of fresh starting material. In this connection it may be worth noting that *C. latialis* might possibly yield crepin in much larger quantities.

The encouragement derived from the earliest studies and efforts in interspecific hybridization led to a definite plan for assembling as many as possible of the known species of *Crepis* in living condition. As a result of extensive correspondence with the directors of botanic gardens throughout the world and with botanical collectors in many countries, the collection of living species increased rapidly. In 1920, 22 species were under cultivation at Berkeley; and in 1921, 29 species were grown. Since that time the number has increased until a total of 113 species of *Crepis* have been cultivated at Berkeley. A few of these species could be grown for only a short time or were represented by only one or two seedlings; but the greater part of them were under cultivation and observation for several years.

In 1920 the author published a paper (Babcock, 1920) intended to call attention to the promising features of *Crepis* as an object of genetic investigation, and at the same time point out the technical difficulties involved in hybridizing such plants. The hope that others would be encouraged to undertake similar research on this group of plants, so that through coöperation more rapid progress might be made, was richly rewarded by the outstanding work of Dr. M. S. Navashin of Moscow. Later, Navashin spent nearly two years at Berkeley collaborating with the present author.

TAXONOMIC STUDIES, 1923-1942

The growing list of accessions of species of *Crepis* and allied genera in the collection of living plants brought to light more and more a state of nomenclatural confusion which made us realize that a thorough revision of the genus was imperative. It was realized that such an undertaking would require a number of years; but it must be admitted that, had the author then appreciated the magnitude of the task, it is doubtful whether he would have undertaken it.

Herbarium studies.—After going over the collection of *Crepis* material then in the University of California Herbarium and reviewing as much as possible of the literature pertaining to the list of species referred to *Crepis* in Index Kewensis, the author spent the year 1924-1925 working in other herbaria. Several months were spent in the eastern United States with headquarters at the Gray Herbarium. Next, a number of European herbaria were visited for the purpose of studying

types, critical material, and as many other specimens as possible, as well as for the purpose of consulting references not available in America. In Berkeley, herbarium studies were continued by means of borrowed specimens (see acknowledgments, p. 29). More than 5,400 herbarium specimens are cited in Part II, and probably as many more have been examined but not cited. In addition, several thousand plants have been observed both in the wild and under cultivation and hundreds have been used in experimentation. Many valuable hints concerning interspecific relationships have come to light through observation of cultivated specimens during various stages in ontogeny.

Author's collections.—The first collections made by the author were in 1925 while on a brief trip through eastern California, Nevada, and southeastern Oregon with Dr. Harvey M. Hall, who was making collections for use in connection with his transplant experiments. Only a few species of *Crepis* were obtained on this trip, particularly *C. occidentalis*, *C. modocensis*, and *C. runcinata*. In 1926 an expedition was made in company with Dr. J. L. Collins, who was then a member of the Division of Genetics, through northern California, central and eastern Oregon and Washington, and western Idaho. Eight different *Crepis* species were obtained, including living material of *C. barbigera*, *C. atribarba*, and several variants of *C. runcinata* subsp. *hispidulosa*. In 1927 an 8,000-mile expedition was made in company with Dr. D. R. Goddard, then of the Department of Botany, University of California, through California, Arizona, New Mexico, Colorado, Wyoming, Yellowstone National Park, Utah, and Nevada. Herbarium specimens and living material of *C. occidentalis*, *C. intermedia*, *C. atribarba*, and numerous forms of *C. runcinata* were obtained. The last-mentioned material proved valuable in checking on the synonymy of this highly polymorphic species. In 1928 an expedition was made through the northern Sierra Nevada from Truckee to Feather River Canyon and out through Plumas and Tehama counties. Seven species, including many forms, were obtained on this trip, and Dr. Navashin preserved young flower heads for cytological study. In 1930 the author made a five months' expedition in the Mediterranean region for the purpose of collecting living material of *Crepis* species. The itinerary included Madeira, Portugal, Spain, Morocco, Algeria, Tunisia, Sicily, Italy, Greece, Crete, Corsica, Majorca, and the southern Pyrenees. Thirty-three species or subspecies were obtained, including roots or seeds of most of them. Through the kind coöperation of the Quarantine Service of the United States Department of Agriculture, the several packages of roots collected on this expedition were forwarded to California promptly, making it possible for each species to be brought into cultivation and to be examined cytologically. Through the kindness of acquaintances made in Algiers (Dr. René Maire), in Greece (M. Guiol and Miss S. P. Topali), and in Spain (Sr. Ramon Sala and, through him, Dr. P. Font Quer and others), additional very valuable material, including several new species, were received in later years. In 1931, 1932, and 1934 short excursions were made in California and Washington where other material of the American species was obtained. In 1936 another expedition was made in the northern Sierra Nevada in company with Dr. G. L. Stebbins, Jr., who was then associated with me in the *Crepis* investigations on a grant from the Rockefeller Foundation. Detailed field studies, including castration experiments and cytological preparations, were made on the *Crepis* species found in Sierra Valley, and collections were made from there northward into the Feather River Canyon. Other sources of living material of *Crepis* are listed below under acknowledgments.

COMPARATIVE MORPHOLOGY THE BASIS OF PHYLOGENY

It is important at the outset to make perfectly clear that the systematic treatment of *Crepis* presented in this monograph rests primarily on comparative morphology. Unfortunate misunderstandings have arisen through misinterpretation of some of the earlier publications on the relations between the chromosomes and phylogeny in this genus. It has even been stated that our phylogenetic conclusions were based on chromosome number alone. Nothing could be further from the truth. In all of our earlier studies, attempts were made to coördinate the evidence from cytology and genetics with the best existing taxonomic treatments of the genus as a whole, found in de Candolle's *Prodromus*, Bentham and Hooker's *Genera Plantarum*, and Engler and Prantl's *Pflanzenfamilien*. These classical works were of course based exclusively on morphology. At the same time, more critical study of morphological details soon revealed serious discrepancies in those older attempts at a taxonomic treatment of this genus; for example, the recognition of *Crepis pulchra* and *C. palaestina* as two monotypic genera, *Phaecasium* and *Cymboseris*. It must be admitted that it was only after finding that the chromosomes of the two species were practically identical in number, size, and shape that a more critical examination of their morphology was made. This evidence on the chromosomes was supplemented by the demonstration that the two species cross readily and the F_1 hybrids are fairly fertile. Then, it was found that the chief reason for the misconception of the older taxonomists was their overemphasis on differences in shape of the fruits. It was also found that *C. pulchra typica* itself is variable in the shape of its marginal achenes (those adjacent to the inner involucral bracts) and that in some forms of this subspecies the marginal achenes are strongly compressed and resemble those of *C. palaestina*. In this monograph, therefore, these two species will be found in the same subgroup of the same section which bears the name of the older of the two monotypic genera mentioned above, *Phaecasium*. A great deal of the confusion which has arisen in the early taxonomic works on *Crepis* has resulted from such overemphasis on one or a few differences and from failure to recognize fundamental resemblances. This will suffice to illustrate how the evidence from comparative morphology, cytology, and genetics has been combined in the determination of interspecific relationships in *Crepis*.

The question of the relative importance of the various criteria of taxonomic and phylogenetic relations may still be open to debate. Smith (1933), in his cytotaxonomic treatise on *Primula* states: "I believe that the last word lies with the morphology. But I can record without hesitation my obligations to the cytologist." What is true of cytology may also be true, and in many instances to a greater degree, of genetics, experimental taxonomy, and geographic distribution. But it must be emphasized that, up to the present time, less than 60 per cent of all the known species of *Crepis* have been brought into cultivation and thus been available for cytologic and genetic research. Comparative morphology, therefore, is of necessity the primary basis of classification in this monograph.

RESEARCH ON THE CHROMOSOMES, 1918-1942

In order to give the reader a concrete notion of the morphological contrasts between the most primitive and most advanced types of *Crepis* species, one of each is shown in the frontispiece, in which all objects are reproduced to the same scales. *Crepis sibirica*, with 5 pairs of chromosomes, has primitive morphological characteristics. It is a strong perennial with horizontal rhizome, large lyrate leaves, few large heads with very large florets and achenes, and the involucre consists of many

large bracts which remain unchanged at maturity. *C. suberostris* subsp. *typica* represents the most advanced species in the genus having 5 pairs of chromosomes. It is a short-lived annual of the littoral sand dunes of Algeria. Its leaves are dissected, its flower heads are numerous and small, and the specialized involucre, having only a few small bracts, becomes much thickened at maturity. These striking morphological and physiological differences in the two species are the result of evolution within a group of *Crepis* species having the same chromosome number.

Two species having different chromosome numbers are also illustrated (figs. A and B). The differences in size and habit of the plant, in size of the heads, florets, fruits, etc., are so obvious it seems hardly necessary to point them out. The primitive species, *C. geracioides*, is a montane perennial which is endemic in the southern Balkan Peninsula. The advanced species, *C. seneciooides*, is a precocious desert annual which has been collected at a number of stations scattered along the Egyptian-Tunisian littoral. Since, on morphological grounds, it is the most advanced species in the genus, it has been used to illustrate the extreme reduction in size which has accompanied development of the annual habit, the extreme precocity, and the remarkable longevity of the tiny achenes, all of which adapt it so well to desert conditions. The fact that these two species, which represent the earliest and latest stages in a very long developmental history, now exist on opposite sides of the Mediterranean Sea, which is only some 600 kilometers (400 miles) wide in this region, is sufficient to pique one's curiosity concerning whence and how they came to be there. The present volume attempts to synthesize the evidence and to derive the most probable hypothesis explaining the present distribution of *Crepis*.

Progress in the studies on the chromosomes of *Crepis* was marked by the publication of papers by Rosenberg (1918, 1920), Navashin (1925, 1926, 1927), Mann (1925), Babcock and Mann Lesley (1926), Hollingshead and Babcock (1930), Babcock and Cameron (1934), Babcock, Stebbins, and Jenkins (1942), and Babcock and Jenkins (1943). All of these papers except the last two are reviewed either by Babcock and Navashin (1930) or by Babcock (1942). Following is a general summary of the information available up to the present, arranged topically.

Chromosome numbers.—On the basis of chromosome numbers alone, this genus consists of two different groups of species: the American species, which have, excluding *C. nana* and *C. elegans* of section 12, the base number, $x = 11$, and the Old World species, none of which has this number. These 10 polyplid American species are discussed below (see p. 22 and Part II, sec. 15). Of the other 103 species which have been studied cytologically, only 6 are polyploids. These consist of 3 tetraploids with $x = 4$ and 3 octoploids with $x = 5$. The remaining 97 species are diploids, which are classified, according to their haploid numbers, as follows: 3 species with $n = 3$, 58 with $n = 4$, 19 with $n = 5$, 14 with $n = 6$, and 3 with $n = 7$.

The 3-paired species include the well-known *C. capillaris*, along with *C. fuliginea* and *C. Zacintha*. It is improbable that many more *Crepis* species having as few as 3 pairs of chromosomes will be discovered. Apparently, $n = 3$ represents an end point in an evolutionary process resulting in reduction in chromosome number. It is noteworthy that these three species, on the basis of comparative morphology, are among the most advanced in the genus.

The three species with $n = 7$, together with four others classed with them because of morphological similarity, comprise the section *Ixeridopsis* which is not among the most primitive sections of the genus. It was suggested by Babcock, Stebbins, and Jenkins (1937) that there is a close genetic connection between these 7-paired *Crepis* species and the 7-paired *Ixeris alpicola* which came about as a result of hybridization between the two genera when they were in a formative period, a



Fig. A. *Crepis geracioides*: a, plant, $\times \frac{1}{2}$; b, flower head, $\times 2$; c, a floret lacking the ovary, $\times 4$; d, trichome from the corolla tube, $\times 100$; d, anther tube slit and opened out, $\times 8$; e, detail of anther appendages, $\times 32$; f, g, 2 achenes and a pappus seta from each, $\times 8$; h, h', 2 inner involucral bracts showing outer and inner faces, respectively, $\times 4$; i, haploid set of chromosomes, $\times 1500$.



Fig. B. *Crepis senecioidea*: a-c and k, plants and parts, $\times \frac{1}{2}$; d, m, florets lacking the ovary, $\times 4$; e, n, anther tubes slit and opened out, $\times 8$; f, o, details of anther appendages, $\times 32$; g, h, p, q, achenes and single pappus setae, $\times 8$; r, haploid set of chromosomes, $\times 1500$.

suggestion compatible with the morphology and geographic distribution of the two groups. This section, therefore, need not be considered further in connection with the history of the main part of the genus.

The remaining diploid species have $n = 4$, 5, or 6, with 4 greatly predominating. However, the nine most primitive species in the genus, as determined from both plant morphology and chromosome morphology, have either 6 or 5 pairs of chromosomes. The most primitive chromosome numbers in *Crepis* are 6 and 5. The great predominance of the number 4 means simply that reduction in chromosome number has accompanied differentiation and speciation along with morphological re-

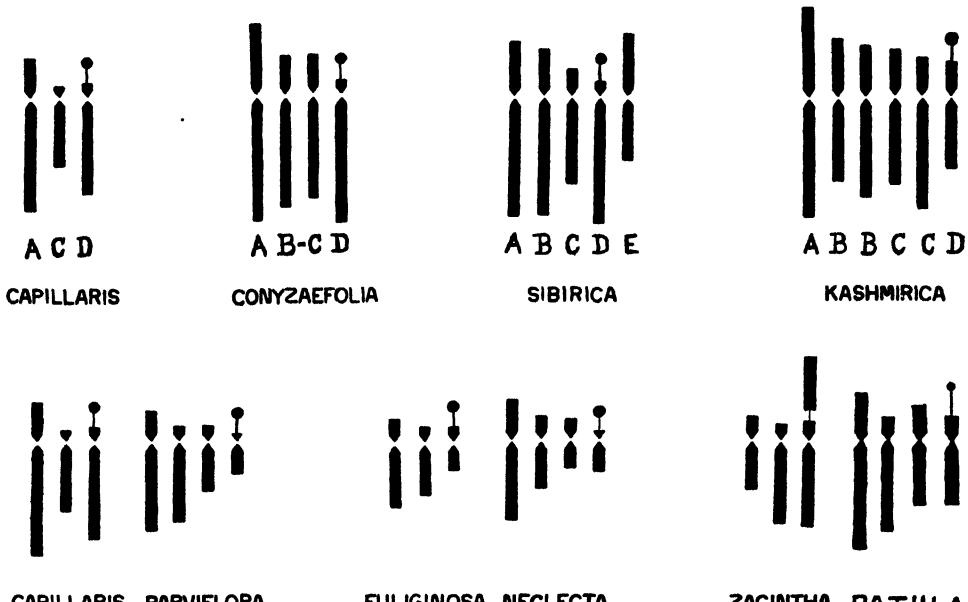


Fig. 1, upper row. Idiograms of four species of *Crepis*. Capital letters indicate the various chromosome types. In *C. conyzaeifolia* it is impossible to distinguish between the B and C chromosomes from their gross appearance in somatic cells. In *C. kashmirica*, with 6 pairs of chromosomes, no E chromosome is present, but there are two each of B and C types. Lower row. Idiograms of the three 3-paired species and the most closely related species of each.

duction and specialization in this genus. Many variations in the typical diploid chromosome numbers have been reported. These are reviewed by Babcock (1942, pp. 148-149).

Karyotypes.—The term karyotype is used here to designate the gross structure of the chromosomes, following Levitsky (1924). A diagrammatic representation of a haploid or basic chromosome set is an idiogram. The original work of Navashin (1925) on *Crepis* karyotypes dealt with 3-paired, 4-paired, and 5-paired species. For purposes of comparison he labeled the members of the idiograms with capital letters, a device still used in describing *Crepis* karyotypes. The complement of a species with $n = 5$ was found to consist of 4 pairs, with a subterminal spindle-fiber attachment or centromere, whereas the fifth pair has a median or nearly median centromere. The one (of the four with subterminal centromere) having the longest proximal arm was designated A, that with the next longest proximal arm was usually B, that with the next longest proximal arm was usually C, and the D chromosome has an extremely short proximal arm or "head" bearing a satellite. The medianly con-

stricted member was labeled E. The idiogram of *Crepis sibirica*, shown in figure 1, has these 5 members. As a matter of fact, the distinctions between type B and type C, as well as between type B and type A, are sometimes arbitrary; but in many 5-paired species it is easy to distinguish definitely between the 5 members of the karyotype. In the 4-paired species studied by Navashin the E chromosome was always lacking; and this has been found to be generally true of the 4-paired species of *Crepis* with a few exceptions, such as *C. oporinoides* of section 10 (Part II, fig. 112), the species of section 19 (Part II, figs. 192–201), in which the A chromosome has a median centromere, and *C. neglecta*, *C. corymbosa*, and *C. Suffreniana* of section 24 (Part II, figs. 246, 247, 251). In the idiogram of *C. conyzaefolia*, shown in figure 1, it is very difficult to distinguish between the B and C chromosomes by the length of the proximal arms, and their distal arms are nearly the same length. In a primitive 6-paired species, such as *C. kashmirica*, 4 of the chromosomes fall into the B or C classes and there is no E chromosome present. Thus, the original scheme of Navashin requires some modifications even for the purpose of labeling the chromosomes according to their gross appearance.

In *C. capillaris* (fig. 1) there are no chromosomes corresponding in appearance to the B and E types; therefore, the three elements present were labeled A, C, and D by Navashin. But, if it is assumed that the 3-paired species were derived from 4-paired ancestors (a necessary assumption if 3 is an end point in a progressively reductional series), then the letters used to designate the three elements may not represent the same chromatin material as in its close relative, *C. parviflora*, or their common ancestor (fig. 1, lower row). It has not yet been possible to compare the chromosomes of *C. capillaris* and *C. parviflora* by means of cytogenetic research on their hybrid; but in *C. fuliginosa* and its nearest relative, *C. neglecta*, this has been done by Tobgy (1943), with the result that it can be stated definitely that the C chromosome of *C. neglecta* is missing, as a separate chromosome, in *C. fuliginosa*, although part of its component material is now present in the B chromosome of this species. In other words, we are certain that the A, B, and D chromosomes of *C. fuliginosa*, considered as entities, are homologous with the A, B, and D chromosomes of *C. neglecta*. This important discovery is discussed below, under karyotype evolution. When the chromosomes of *C. Zacintha* and its closest relative, *C. patula*, are compared (fig. 1), the difficulty of homologizing the chromosomes of the two species from their gross appearance is obvious. Thus, it becomes clear that, although labeling the chromosomes of various species has been a useful device for certain purposes, it must be clearly understood, as Navashin and Gerassimova (1935, 1936) have pointed out, that homologizing the chromosomes of different species solely on the basis of their gross appearance is likely to lead to confusion.

Chromosomes and phylogeny.—The phylogenetic significance of chromosome number, size, and shape can be interpreted only in relation to or with aid of other criteria. In the first effort to synthesize the evidence from taxonomy and cytology (Babcock and Mann Lesley, 1926), thirty-three species were considered, including *Aethorrhiza bulbosa* and two species of *Youngia* which are now excluded from *Crepis*. Because certain changes in the sections of Hoffmann (in Engler and Prantl's *Pflanzenfamilien*) were found to be necessary in order to coördinate the data on chromosome number and size, a tentative new classification by sections was proposed. Hollingshead and Babcock (1930) reported on sixty-five species, including one species of *Youngia* which is now excluded. Eight of these species were restricted to North America. Four major subgeneric groups, Paleya, Barkhausia, Catonia, and Eucrepis, were recognized, and a tentative phylogenetic scheme was drawn up with Paleya (*C. albida*) assumed to represent the ancestral form. Seventeen sub-

groups or sections were recognized on the combined evidence from comparative morphology and the chromosomes. One of these comprised seven American species, with somatic chromosome numbers ranging from 22 to 88. It was suggested that they originated from hybridization between Asiatic species having 4 and 7 pairs or 5 and 6 pairs of chromosomes, followed by amphidiploidy. The general conclusion was reached that, in each section of the genus, morphologically similar species have similar chromosomes and there is a fairly close parallelism in *Crepis* between number and morphology of the chromosomes and phylogenetic relationship.

Four years later, Babcock and Cameron (1934), after comparing the karyotypes of 108 species and considering the evidence on relationship provided by other criteria, concluded as follows: (1) morphologically similar species have similar chromosomes; (2) similarity in chromosome types and in details of size and shape is an index of phylogenetic relationship (when used, of course, in connection with other criteria); (3) both increase and decrease in chromosome size have occurred in the evolution of the genus; (4) a general tendency toward reduction in size of the chromosomes exists concurrently with reduction in size of the plant and reduction or specialization of parts; (5) many changes have taken place in chromosome shape, as determined by relative length of the arms, and by these differences chromosomes of the same types from different species can be identified in hybrids; (6) this fact makes it possible, by analysis of the haploid karyotype, to determine the mode of origin of certain species; and (7) chromosome number and morphology are taxonomic criteria of great value in this genus. But the chromosomes must be used in connection with other available criteria, such as comparative morphology, genetic data, and geographic distribution. Certainly absolute identity of the chromosomes cannot be set up as of paramount importance in the classification of species, for species are known in which different forms exhibit differences in number, size, or shape of the chromosomes. The genus is still evolving and visible changes in the chromosomes are part of the process. Many alterations in specific karyotypes have been induced experimentally and some have arisen spontaneously. These are discussed below (pp. 18-20).

Karyotype evolution.—It has been pointed out (Babcock, Stebbins, and Jenkins, 1942) that there are distinct evolutionary trends in the karyotype diversity in *Crepis* and that these karyotype changes may be summarized under a number of distinct heads.

1) *A progressive decrease in the basic chromosomal number* is the most outstanding karyotype change occurring in the genus *Crepis*. In spite of the fact that most of the species have a basic number of 4, the morphologic and geographic evidence indicates that the primitive number is 6, and those species with 5, 4, and 3 as the haploid number are definitely derived. There are a few exceptions to this progressive decrease in chromosome number which involve either polyploidy or hybridization or both.

2) *Polyploidy* is largely confined to the American species, in which, together with apomictic reproduction, it has resulted in a great diversity of forms, i.e., in large species complexes. In the rest of the genus, doubling of the chromosome number, although having occurred on several occasions, has, on the whole, played a relatively minor role.

3) *An increase in asymmetry* is manifested in two ways: (1) a tendency exists for the more advanced species to have karyotypes made up of chromosomes of unequal lengths; and (2) the more advanced species have chromosomes with a more terminally situated centromere, which leads to a chromosome with one arm longer than the other.

IDIograms showing karyotype evolution in *Crepis* reduction in number, total length and symmetry of the chromosomes

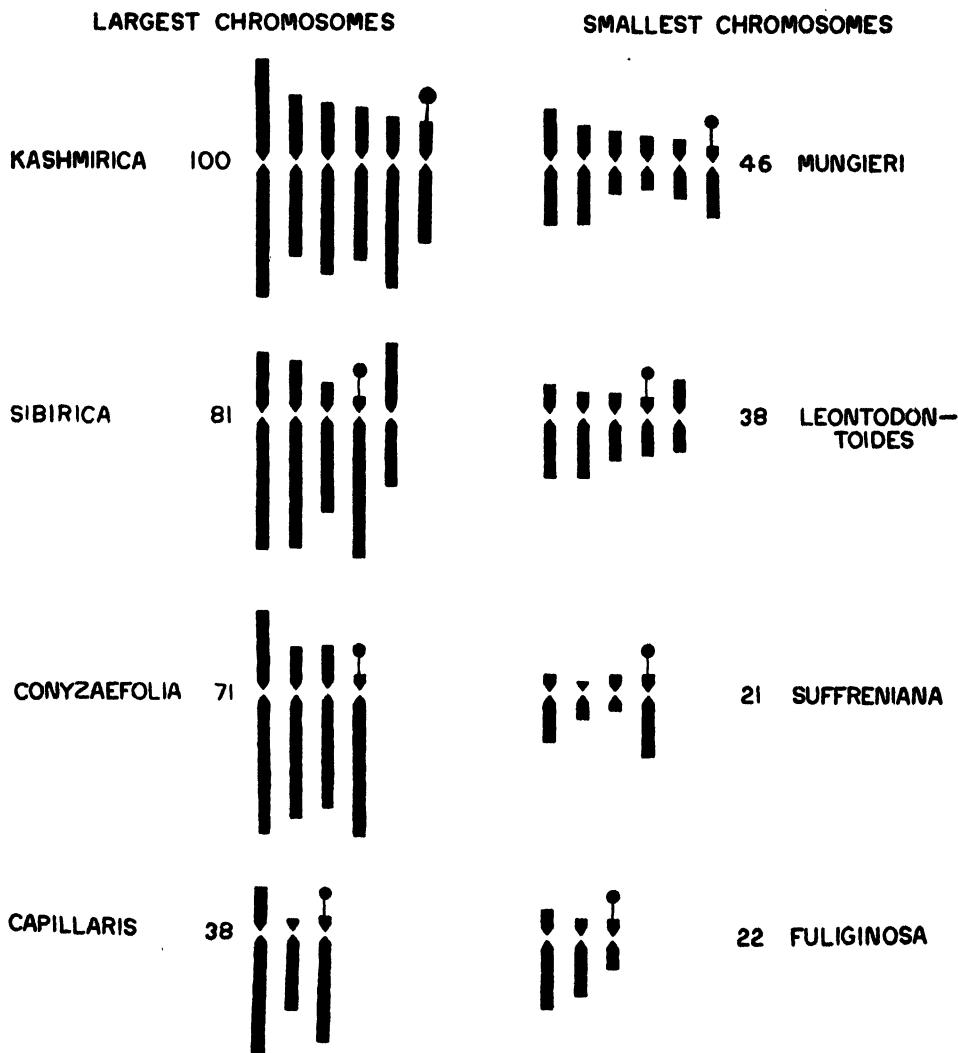


Fig. 2. Idiograms of the species with longest and shortest total chromosome length in each of the four number classes, $n = 6, 5, 4$, and 3. The reduction in symmetry is emphasized by placing the spindle-fiber constrictions on a common baseline in each number class. Using the total length of the somatic chromosomes in *C. kashmirica* as a base of 100, the proportional total length of each idiogram is shown by the number between the name of the species and its idiogram. With respect to the absolute size of the individual chromosomes, these idiograms are accurate only to a degree sufficient for purposes of the present discussion.

4) *A decrease in chromosome size* is the least well marked of the evolutionary trends. It is to a limited but not invariable extent correlated with a parallel decrease in total size of the plant. It is frequently associated with a specialized and restricted distribution of the species.

Babcock and Jenkins (1943), reporting on 113 species of *Crepis* representing twenty-three of the twenty-seven sections recognized in this monograph, reached the following conclusions:

1) The general trends of karyotype evolution in this genus are: (1) decrease in chromosome number; (2) increase in asymmetry of the chromosomes; and (3) decrease in chromosome size. These trends are all indicated by the idiograms of the eight species shown in figure 2 (see legend). These trends in karyotype evolution have occurred independently of processes resulting in morphological change.

2) Decrease in chromosome number has been progressive, from $n = 6$ to $n = 3$. The process went on step by step, through the loss of one chromosome at a time; and each step occurred independently on several different occasions. The evidence from *Crepis* supports Navashin's (1932b) dislocation hypothesis; that is, change in chromosome number through reciprocal translocations. In addition to the main trend of decrease in number, there have also been increases in number in certain restricted groups, such as amphidiploid hybrids and polyploids of various types.

3) Chromosome asymmetry is a further consequence of unequal reciprocal translocations; this, in spite of the fact that once the initial asymmetry is established the process does produce an opposite trend toward symmetry. In the long run the latter tendency predominates to a greater or less degree. Although it is impossible to recognize in *Crepis* a phylogenetic sequence on the basis of chromosome asymmetry, yet, in general, the more primitive species in the genus have more symmetrical chromosomes than the more advanced species (see fig. 2).

4) The decreasing trend in chromosome size also fails to follow a strict phylogenetic sequence. Although there is a general tendency for reduction in chromosome size, together with concurrent reduction or specialization of the plants and with a shortening of the length of the life cycle, yet, at the same time, there are numerous exceptions. The factors influencing this trend in *Crepis* are evidently complex, since they may reflect different physiological states which in turn may be influenced by various environmental factors. But it may be assumed that the physiological differences which characterize the species are gene determined; and therefore gene mutations may furnish the basis for the trend in decreasing chromosome size.

On account of the existing diversity in usage of the terms gene and gene mutation, it seems advisable, for sake of clarity, to define them here.

The term *gene*, as used in this monograph, means one of the hereditary units which make possible the particulate nature of inheritance, the phenomena of Mendelism and linkage. A more precise definition, in physical terms, need not be essayed here. It is well known, however, that the genes exist in the chromosomes; also that a chromosome includes a series of regions which are marked off by points or zones of potential breakage. Any such region makes up only a very small part of the length of a chromosome, is self-reproductive, and has a specific controlling action on cell physiology. The idea that each gene is a material entity of some sort and is situated in a particular gene region is a generally used concept.

Gene mutation means any change in a gene region which alters its action in cell physiology and is maintained in chromosome reproduction; it includes, therefore, those aspects of alterations in the linear order of gene regions known as position effects. Evidently such alterations also occur within gene regions (Goldschmidt, 1945, pp. 526-527). According to Huxley (1943, pp. 50-51), "a gene mutation will

then be any intrinsic change in substance or structure affecting the mode of action of one of these unit regions"; and "gene mutations (including position effects) appear to be the most important source of novelty in evolution. . . ."

GENETIC AND CYTOGENETIC RESEARCH, 1923-1942

It was from Dr. H. M. Hall that the author received the first suggestion regarding the application of genetical methods to the solution of taxonomic problems. At Hall's invitation the present author undertook genetic research on the common hayfield tarweeds of California which led to a joint publication (Babcock and Hall, 1924) in which the evidence from experimental genetics was combined with evidence from ecological and herbarium studies in working out a difficult problem in plant systematics. Along with the pioneer work of Dr. J. Clausen on *Viola* (1921-1922), these investigations comprise the earliest efforts known to the present author to synthesize the evidence from research on genetics, comparative morphology, and geographic distribution in attempting to discover a truly natural basis for the systematic treatment of a group of plants. Hall's point of view in this early work was essentially that of the "new systematics" of today, since he held that the taxonomist should think in terms of evolutionary processes and should learn to treat his morphologic criteria as dynamic rather than static. In short, it was Hall's emphasis on the phylogenetic viewpoint in taxonomy which led the present author to undertake, with the aid of various co-workers and students, the investigations on the genetics and cytogenetics of *Crepis* which have made possible the present attempt at a phylogenetic treatment of this genus. Since a complete historical record of all this research would require too much space and would be of doubtful value, the following topical treatment presents those results of the investigations which are of most significance for biosystematics.

The studies on the genetics of various species of *Crepis* have been summarized by Babcock and Navashin (1930, pp. 47-52) and Babcock (1942, pp. 161-162). The actual work was done by a number of different associates, the most important contributions being made by Collins (1924), Hollingshead (1930a), Babcock and Cave (1938), and Jenkins (1939). In general, the Mendelian inheritance of many morphological and of some physiological differences within species was clearly demonstrated; and quantitative differences were shown to be conditioned, as a rule, by multiple genes, although dwarf forms were discovered in certain species to be dependent on a single genic difference.

The first interspecific hybrids in *Crepis* were reported by Babcock and Collins (1920), but, during the following decade, the data on interspecific hybrids accumulated rapidly. The bearing of many of the findings on interspecific relationships was recognized as being so significant that it was decided to concentrate mainly on this phase of genetic and cytogenetic research rather than to attempt to make an extensive genic analysis of any one species. These investigations on interspecific hybrids have been reviewed in part by Babcock and Navashin (1930, pp. 37-43, 53-63) and by Babcock (1942, pp. 161-164, 173-178). The results also represent the efforts of a number of different workers, both at Berkeley, California, and at Moscow, Russia. Many discoveries of importance for the systematics of the genus were made during the course of these investigations. The following deserve to be mentioned because of their bearing on our phylogenetic and taxonomic concepts.

The simple genetic basis of receptacular paleae.—The discovery by Collins (1924) of a plant of *Crepis capillaris* with well-developed paleae on the receptacle and his demonstration that presence and absence of the paleae behave as a pair of Mendelian characters has an important bearing on the delimitation of the genus. The

small genera, *Pterotheca*, *Lagosseris*, and *Rodigia*, had been separated from *Crepis* primarily on the basis of presence of paleae on the receptacle. Now the question arose, since presence or absence of paleae within *C. capillaris* rests on such a simple genetic basis, is one justified in maintaining the three small genera just mentioned? Several years later Mrs. Cave (Babcock and Cave, 1938) found from crosses between *C. foetida commutata* (= *Rodigia commutata*), which has receptacular paleae, and *C. foetida vulgaris*, which has none, that presence and absence of the paleae are dependent on three genes, two primary and an inhibiting one. Thus, the one feature by which the former genus *Rodigia* was separated from *Crepis* was also shown to have a simple genetic basis. The hybrids between *R. commutata* and *C. foetida* were vigorous and highly fertile and they produced vigorous, fertile progeny. Furthermore, the geographic areas of the two entities overlap and intergrading variants occur. Hence, by this one experiment it was shown not only that *Rodigia* should be merged with *Crepis*, but also that the hybrid fertility relations are such that *R. commutata* must be reduced to the rank of subspecies. Finally, since occasional plants of *Crepis sancta* (= *Pterotheca sancta*) have been found which lack paleae on the receptacle, and since the plants are otherwise entirely *Crepis*-like, it has been assumed that both *Pterotheca* and *Lagosseris* should be merged with *Crepis*.

Interspecific lethal genes in Crepis.—An interspecific lethal factor was discovered by Hollingshead (1930a) in *Crepis tectorum*. It was found that some strains of this species, when crossed with *C. capillaris*, would produce only plants which died in the cotyledon stage, whereas others would give all viable offspring, and still others about half-and-half viable and inviable. Further tests proved that this factor behaved as a simple Mendelian recessive. Since normal meiosis in *C. tectorum* is always regular, it may be assumed that this factor is not a structural difference in the chromosomes of the different races of *C. tectorum*, but simply a gene. It was also found by Hollingshead (1930a) that, in crosses between *C. tectorum* and *C. bursifolia* and between *C. tectorum* and *C. leontodontoides*, both viable and inviable progeny occur in the proportions expected if the *C. tectorum* lethal were effective. But her data on *C. tectorum* \times *C. vesicaria taraxacifolia* and on *C. tectorum* \times *C. setosa* indicate that the lethal gene is ineffective in these hybrids. Certain other data on interspecific crosses not involving *C. tectorum* indicate that similar lethals may exist in other species of *Crepis* not yet subjected to genetic investigation. It should be noted that some of the strains of *C. tectorum* used by Hollingshead were of wild origin and from widely separated localities. Evidently this lethal originated either long ago or more than once in the history of this species. Since the closest relatives of *C. tectorum* are *C. Bungei* and *C. ircutensis*, it would be of interest to investigate the behavior of hybrids between these three species. If the lethal gene proved to be effective in hybrids between *C. tectorum* and the other two, the probability of its importance in the evolution of *C. tectorum*, which is the most advanced of the three species, would be greatly strengthened. Only three other cases of interspecific lethals or semilethals have been reported. One is in cotton (Hutchinson, 1932; Silow, 1941), and two are in *Drosophila* (Crow, 1942; Patterson, 1944). The evolutionary significance of the four cases is discussed by Patterson (*op. cit.*, pp. 219-220).

Crossability, hybrid fertility, and taxonomic relationship.—We are here concerned with the correlation between the genetical evidence and the degree of taxonomic relationship of the species as determined from comparative morphology. Interspecific hybridization has been conducted on an extensive scale in *Crepis*. The compatibilities of 35 species between which hybrids were obtained before 1930, as indicated by seed production under open-pollination, were reported by Babcock

and Navashin (1930). Between 1920 and 1939 data were obtained on about 200 interspecific hybridizations involving 55 species. The data on crossability, viability, and fertility are presented in chapter 3 (pp. 58–61). In general, as would be expected, hybrids between species which are less closely related, as judged from morphology, tend to be weak and sterile or, if vigorous, to be sterile or of very low fertility; whereas hybrids between more closely related species tend to be vigorous and more or less fertile. The evidence obtained from interspecific hybrids in *Crepis* and its bearing on taxonomic concepts are summarized in chapter 3 (pp. 52–58). Negative evidence on crossability may be of slight significance, but positive evidence in the form of hybrids, together with data on their fertility, is a valuable criterion of relationship. Much remains to be done to amplify the evidence on crossability and hybrid fertility. Of considerable significance is a hybrid between *Crepis sancta* of section 22, *Pterotheca*, and *C. leontodontoides* of section 14, *Mesophyllum*, growing in our greenhouse now (June, 1943). The latter species has been especially useful in obtaining interspecific hybrids. Several earlier efforts to make this cross had failed; but now a vigorous hybrid plant provides additional evidence of the close genetic relationship of *Pterotheca* and another section of *Crepis*.

Chromosome pairing in species and hybrids.—The diploid species of *Crepis* in general are highly regular in the behavior of their chromosomes during meiosis. Perfect pairing of the chromosomes was observed in *C. aspera* and *C. bursifolia* by Clausen (Babcock and Clausen, 1929). Complete or nearly complete regularity was reported in *C. tectorum* by Hollingshead (1930b); in *C. syriaca* by Cameron (1934); in *C. foetida* and *C. eritreensis* by Babcock and Cave (1938); in *C. divaricata*, *C. Noronhaea*, *C. canariensis*, and *C. vesicaria* by Jenkins (1939); and in the sexual, diploid forms of *C. acuminata* and *C. occidentalis* by Stebbins and Jenkins (1939). Frequent failure to conjugate on the part of the members of one of the 5 pairs of chromosomes in a certain strain of *C. foetida rhoeadifolia* was explained by Poole (1931) as probably due to a constantly observable difference in size of the satellite borne by the members of this pair. In a certain strain of *C. capillaris*, known as the "X-strain," Hollingshead (1930b) observed univalent chromosomes at metaphase in from 12 to 44 per cent of the pollen mother cells of different plants growing under the same favorable conditions. It was discovered by Richardson (1935) that the occurrence of univalents at first metaphase in this strain is caused by failure of chiasma formation between homologous chromosomes which were found to be regularly associated in earlier (pachytene-diakinesis) stages. This, however, is exceptional, for such marked variations in metaphase pairing is not generally characteristic of diploid species.

The evidence on chromosome pairing in the first meiotic division in pollen mother cells of eleven interspecific *Crepis* hybrids was reviewed by Babcock and Emsweller (1936). Comparison of the average amounts of pairing at first metaphase in these hybrids leads to the conclusion that the genic complements of the fourteen species involved are all more or less homologous. This inference is consistent with the evidence on chromosome morphology in the genus, on geographic distribution, and on the results of the research on small groups of closely related species discussed above. This evidence on metaphase pairing in interspecific hybrids, therefore, supports the conception that the species of *Crepis* had a common origin and are still more or less similar in genetic constitution. At the same time it should be noted that more recent and detailed research on certain other interspecific *Crepis* hybrids has shown that meiotic irregularities in these hybrids are caused by differences in the structural arrangements of certain segments in the chromosomes of the parental species (see below, under the role of structural rearrangements in differentiation).

Polyploidy, autosyndesis, and new species.—Although polyploidy is not of major importance in the genus as a whole, yet it does exist in certain species of *Crepis* and, in fact, has played an important role in the evolution of most of the American species (see below). One of the few Old World polyplloid species is the widespread *C. biennis*, which was among those acquired early in the history of these investigations. *C. biennis* usually has 40 chromosomes in its somatic cells. When it was crossed with *C. setosa*, which has 8 chromosomes, the F_1 hybrids were found by Collins and Mann (1923) to have, as expected, 24 chromosomes. But, at metaphase in the pollen mother cells of these hybrids, they observed 10 pairs and 4 single chromosomes; and further investigation proved that the 10 pairs were formed by the 20 from *C. biennis* and the 4 singles were those contributed to the hybrid by *C. setosa*. This automatic pairing of the chromosomes of *C. biennis* among themselves in the hybrid was a most striking example of autosyndesis, a phenomenon discovered by Rosenberg (1909b) in *Drosera*. All of the evidence from this hybrid and its derivatives indicates that *C. biennis* is an octoploid species with the base number $x = 5$, a conclusion of importance in establishing the phyletic relations of *C. biennis*. As a result of autosyndesis among the *C. biennis* chromosomes and random distribution of the *C. setosa* chromosomes, the gametes of the F_1 hybrids received 10 *biennis* + 0 to 4 *setosa* chromosomes. Among the selfed progeny of such a hybrid there was one plant with 24 chromosomes which proved to be 10 pairs from *C. biennis* and 2 pairs from *C. setosa*. This new type combined characteristics from both parent species, and the first few generations obtained from the original plant were fairly uniform. Accordingly, it was named *C. artificialis* (Collins, Hollingshead, and Avery, 1929). In later generations, however, considerable variation in chromosome numbers was found among the progenies of selfed plants; and, as a result of testing selected individuals, Jenkins (unpublished) has obtained strains with various diploid numbers ranging from 20 to 36. Some of these strains appear to be fairly uniform morphologically, and it is possible that they might become established as natural species if given an opportunity in the wild. Although these investigations have revealed one process by which new species may originate in nature, yet there is no evidence that any existing *Crepis* species did originate from hybrids between species with such widely different chromosome numbers as those of *C. biennis* and *C. setosa*. However, a somewhat similar process involving interspecific hybridization seems to have been of great importance in the origin of several American species of *Crepis* (see below).

The evolutionary role of gene mutations.—Gene mutations, such as those causing naked receptacles and interspecific lethals, are doubtless of importance in the evolution of *Crepis*; but it is the great mass of less obvious mutations, causing small changes but affecting any part of the plant, which provides most of the material for intraspecific differentiation. The evidence from *Crepis* certainly indicates that, given some kind of isolation (cf. pp. 147-151), intraspecific differentiation leads eventually to the origin of new species. Many species of *Crepis* are polymorphic and twenty species consist of more or less well-defined geographic races or subspecies. In several of these which have been investigated cytogenetically the chromosomes of the subspecies appear to be identical and evidently differ from one another only with respect to certain genes. Such species are probably in process of differentiation as a result of mutation accompanied by selection under varying environmental conditions. Excellent examples are *C. foetida* and *C. vesicaria*, each of which is actually a superspecies composed of several distinct but interfertile subspecies; each of these subspecies has a wide distribution, but sufficient overlapping allows swarms of intergrading hybrids to occur. One can imagine what would happen if some sort of barrier, such as intersterility, were to separate

one of the subspecies from those with which it comes in contact. Its status would change to that of species in course of time, if not rapidly. This is actually what has happened in two groups of very closely related and rather thoroughly investigated *Crepis* species; but, here, the isolating barrier is geographic instead of genetic.

Crepis foetida and two close relatives.—In addition to *C. foetida*, Babcock and Cave (1938) studied *C. eritreensis* and *C. Thomsonii*. From their geographic distributions (fig. 203), it is clear that the two latter species are widely separated from each other and from *C. foetida*. *C. Thomsonii* and *C. foetida* have closely similar karyotypes, and the chromosomes of *C. eritreensis* exhibit only small differences from those of the other two species. In F_1 hybrids between any two of these species the pairing of the chromosomes in meiosis is practically perfect, indicating no large structural differences between the species. However, a comparison of meiosis in F_1 hybrids between each of these species and one 4-paired species (Sherman, 1946) indicates the existence of some structural differences in the chromosomes of these three species. Morphologically, the plants are sufficiently similar to be placed in the same subgroup of the same section; yet the genetic evidence shows that they differ in numerous genes. The fertility of the F_1 hybrids varies from very high in some to very low in others. It is sufficient, however, so that if the geographic ranges could overlap, the species would probably become merged and then *C. eritreensis* and *C. Thomsonii* would have to be treated as subspecies. But these species do not approach one another closely at present, and there is no reason to anticipate that they will meet for an indefinite period of time. To this fact may be added the following reasons for considering *C. eritreensis* and *C. Thomsonii* to be species: (1) they differ from *C. foetida* in many, not few, genes; (2) F_2 data from crosses show that these two species differ more from *C. foetida* in respect to self- and cross-compatibility than the various strains of *C. foetida* differ among themselves; (3) they both differ from *C. foetida* in the genes conditioning color of the ligules and the presence of red ligule teeth; (4) *C. eritreensis* has monomorphic achenes, while *C. Thomsonii* and *C. foetida* have dimorphic achenes; (5) both species differ from *C. foetida* and from each other in certain other morphological features and both have a shorter life cycle than the most precocious form of *C. foetida*; and (6) both species show more morphological and physiological resemblance to *C. foetida vulgaris* than to the other two subspecies of *C. foetida*, even though the former subspecies is farther removed from them geographically. This indicates a phylogenetic connection fairly remote in time. During an ensuing epoch, barring a catastrophe and assuming continuation of the present balance between evolutionary pressures, these species may become much more distinct from *C. foetida* than they are at present through the accumulation of gene mutations.

Four insular endemics.—The other group of closely related species was investigated by Jenkins (1939). The group consists of four species: *C. canariensis* of Lanzarote and Fuerte Ventura of the Canary Islands; *C. divaricata* of Madeira; *C. Noronhaea* of Porto Santo Island near Madeira; and *C. vesicaria andryalooides* also of Madeira but well isolated from *C. divaricata*. *C. vesicaria andryalooides* is treated as a subspecies because *C. vesicaria taraxacifolia* has been introduced into Madeira, because it has invaded the area occupied by subsp. *andryalooides*, and because the two have become merged in a hybrid swarm. The facts about these five entities, with respect to morphological similarities and differences, chromosome similarity and meiotic regularity in parents and hybrids, and the genetics of quantitative and qualitative differences, are practically identical with those concerning the three species considered above. Among the five entities, Jenkins found a great many morphological differences affecting all parts of the plant. In his experimental

F_1 hybrids he found the average fertility, as indicated by percentage of seed setting in the open, was 25 to 50 per cent. The least fertile hybrids had only 1 to 2 per cent, and the most fertile 50 to 75 per cent, as compared with nearly 100 per cent in all of the parents. Thus, interfertility between all four species has been definitely though not completely reduced. The available cytological evidence certainly indicates that the five entities have a similar arrangement of genes in each of their 4 chromosomes. The cytological evidence, however, does not include detailed pachytene studies, and it is quite possible that minute structural differences are also present in these species. The situation is comparable to that reported by Silow (1944) for *Gossypium arboreum* and *G. herbaceum* in which "there is on the whole so extremely little cytological irregularity between the species that their differences must be referred, in the main, to a genetic basis." Therefore, the varying degrees of genetic isolation which have already developed in these species must be largely, if not wholly, the result of gene mutations.

Other evidence.—Babcock and Navashin (1930) report the result of crossing two diverse forms of *C. capillaris*, a low diffuse plant found in the Pyrenees, and a robust variant from northern Europe. The F_1 was intermediate in size and habit and was not over 50 per cent fertile. Also, in *C. tectorum*, a cross between a Scandinavian dwarf variant (var. *pygmaea*) and a tall form from Russia gave an intermediate F_1 with 50 to 60 per cent estimated fertility. Meiosis not having been studied in these hybrids, the evidence is incomplete. But, with more extensive research on intra-specific hybrids, probably many more cases of partial sterility between subspecific entities having no detectable structural differences in their chromosomes would come to light. From the evidence submitted, it is clear that in *Crepis*, at least, gene mutations comprise a genetic process of major importance in interspecific differentiation. In addition to their function in building up intra- and interspecific sterility, they are omnipresent and may at any time operate to supplement and extend the other genetic processes concerned in the evolution of species.

Experimental induction of mutations.—The experimental work on the induction of mutations in *Crepis* has been directed mainly toward the production of structural changes in chromosomes; but, in connection with some of this work, new gene mutations have been noted. Two general methods have been used, namely, the application of x-rays and the aging of seeds. All of the published research on *Crepis* in this field has been done by Russian botanists.

Effects of x-rays and neutrons on the chromosomes.—Navashin (1931a, b, c) initiated experimentation with the effects of x-rays on *Crepis*, using *C. tectorum*. Various categories of chromosomal alterations were observed, including translocations between nonhomologous chromosomes, which are the most important type of structural change in the evolution of *Crepis*. Levitsky and several associates (1931-1934), reporting experiments with *C. capillaris*, assumed that all the translocations observed were nonreciprocal. But, later, Levitsky (1935) concluded that the translocations he observed in *C. capillaris* were mostly, if not all, reciprocal. From the analysis of somatic plates in which the "shortening curves," representing changes in the longer arm of all three chromosomes, are compared, he concluded that breaks leading to reciprocal translocations occur shortly before the metaphase stage of cytokinesis. Korjukae (1940) corroborated Levitsky's conclusion that the translocations induced by x-rays in *C. capillaris* are reciprocal. Levitsky (1937, 1940) also reported numerous other observations on chromosome alterations induced by x-rays, but these need not be discussed here. Kostoff (1943) reports that treating seeds of *C. capillaris* with a total neutron dose of about 20,000 r caused changes in the karyotype in 70 per cent of the cells examined. Most of the dislocations consisted

of fragmentations and translocations, and all 3 chromosomes were involved. Evidence of inversions was also observed.

Effects of the aging of seeds.—The aging of seeds as a cause of chromosomal mutations was first reported by Navashin (1933b), who states that seeds of *C. tectorum* show only 2 to 3 per cent germination when kept six to seven years. Chromosomal translocations were found in 81 per cent of the seedlings. He also reported (1933c) that the process of mutation in resting seeds was accelerated by increased temperature. Shkvarnikov and Navashin (1934) reported that fresh seeds of *C. tectorum*, after exposure to a temperature of 54 to 55° C for twenty, forty, and forty-four days, showed chromosome abnormalities, just as they did when exposed to increasing doses of x-rays. Of 106 roots of surviving plants (from twenty days' exposure), 14 showed chromosome translocations. Navashin and Gerassimova (1935, 1936) reported important additional observations on the chromosomal alterations occurring in the resting embryos of seeds. The evidence does not prove that all the translocations are reciprocal, but this is very probable. Certain of their data furnish good support for the "dislocation hypothesis" of evolution of basic chromosome numbers (see below). Translocations and inversions also probably play an important role in evolution as factors causing physiological isolation (cf. Gerassimova, 1935; Dobzhansky, 1941). Shkvarnikov (1939) reported that temperature, humidity, and other factors cause mutations in stored seeds through the physical and chemical processes taking place in the seeds; and similarly with mature pollen. Mutations of various sorts were observed, including both chromosomal and "point" or gene mutations. He inferred that in nature such variations must occur with high frequency when favorable conditions exist.

Most recently, Navashin, Gerassimova, and Belajeva (1940) analyzed the results of storing seeds of *C. capillaris* and *C. tectorum* for two, three, four, and five years in a basement where temperature and humidity fluctuations were recorded. A striking difference in the two species was observed in the effects of storage on germinating power and viability of the seedlings. As had been observed in earlier work, the seeds of *C. capillaris* showed much greater resistance to the effects of storage. This difference between the two species, it was pointed out, indicates an important adaptation in *C. tectorum*. Whereas *C. capillaris* is a typical annual, and its seeds normally germinate in the spring after 250 to 270 days of dormancy, *C. tectorum* is a "winter plant," that is, its seeds germinate soon after maturation and the vegetative rosettes live through the winter, the plants flowering the following season. (It should be noted that this physiological peculiarity of *C. tectorum* has been of value to the present author as an aid in determining the interspecific relationships of this species.) Since *C. capillaris* was found to be a favorable species, a thorough investigation was made of the occurrence of structural chromosomal mutations in increasing storage periods. In brief, it was found that the percentage of such mutations increased very rapidly after a certain period of time, whereas the percentage of mortality of embryos and seedlings increased uniformly throughout the entire period of storage. From this, it was concluded that an actual biological process was involved in the rapid increase in percentage of mutations; and it was inferred that increased humidity was the determining factor causing the increase in mutations. This led to the suggestion that seeds stored naturally in any place where the temperature was lower and the humidity higher than on the surface of the soil might contain a greater proportion of mutations.

Spontaneous mutations.—Spontaneous structural chromosomal alterations were reported by Navashin (1931c, 1932a, 1933a) in *Crepis*. The significance of such spontaneous mutations was emphasized by him (1931c) as follows: "It is obvious

that any heterozygous dislocation (translocation) would ultimately result in gain or loss of chromatin material in succeeding generations owing to segregation of chromosomes. And, if not incompatible with life, these may result in variations of evolutionary significance. For there can be hardly any doubt that the evolution of *Crepis* species was primarily based upon changes in the quantity of material contained in the individual chromosomes."

The evolutionary role of large changes in chromosome structure.—Structural changes in the chromosomes, leading to chromosomal transformation, alteration of karyotypes, and changes in chromosome number, have long been recognized as of fundamental importance in the evolution of *Crepis* (Hollingshead and Babcock, 1930). In the light of accumulated evidence, the conclusion that this process has been of primary importance in *Crepis*, and probably in several other genera, appears to be warranted. The hypothesis of Delaunay (1926) that reduction in *absolute size* of the chromosomes often accompanies evolutionary advancement is in general agreement with the evidence on phylogeny, as based on comparative morphology of the plants and chromosome size, not only in *Crepis*, but also in *Lactuca*, *Prenanthes*, and *Ixeris* (Babcock, Stebbins, and Jenkins, 1937), even though there are certain exceptions to the general rule. The hypothesis of Levitsky (1931) that primitive species have more numerous chromosomes with *median constrictions*, with the chromosomes comprising the karyotype nearly equal in size, and that, *along with advancing evolution, subterminal constrictions are developed* and the chromosomes become fewer in number and more unequal in size, is supported by the evidence from *Crepis* and from related genera (Babcock, Stebbins, and Jenkins, 1937).

Navashin's dislocation hypothesis.—From her evidence on partial metaphase pairing in hybrids between *Crepis* species with different chromosome numbers and different karyotypes, Avery (1930) inferred that the chromosomes of the different species contained some genetically homologous segments. She suggested a scheme of karyotype transformation, involving reduction in number from 5 to 4, based on several types of structural change. Such evidence, together with the appearance of new types of chromosomes in the progenies of two triploid hybrids in *Crepis*, led Navashin (1932b) to propose his "dislocation hypothesis," which he based on the following facts: (1) chromosome number is conditioned by the number of centromeres which cannot be formed *de novo*; (2) segments of chromosomes may be lost or transferred to other chromosomes and this "dislocation" process may occur in both somatic and germ cells; and (3) the normal effect of a given portion of chromatin does not depend on the particular place it occupies in the chromosome system; and regular pairing in meiosis does not depend on the similarity of whole chromosomes, but on similarity of elements occupying corresponding levels in the conjugants. Hence, *the only conceivable way of changing the chromosome number is by addition or loss of one or more centromeres combined with appropriate dislocation*. Changes in either the plus direction or the minus direction could be explained on this basis. Although the "dislocation hypothesis" assumed nonreciprocal translocations and dealt only with chromosome number as a specific characteristic, yet it did explain changes in symmetry of individual chromosomes and in the relative size of different members in a set. But it leaves unexplained the evolutionary transformations in absolute size and bulk of the chromosomes.

Evidence from structural hybridity.—Evidence showing that structural changes have occurred during the evolution of *Crepis* has continued to accumulate. The most convincing of such evidence has come from the analysis of meiotic irregularities found in interspecific hybrids. Müntzing (1934) studied meiosis in a hybrid between *C. divaricata* and *C. Diocoridis*, each of which species has $n = 4$ chromosomes,

though they belong to different sections (23 and 25). In addition to an average of only 1.8 bivalents at first metaphase in the pollen mother cells, fragments were observed at diakinesis and metaphase, and in some first anaphase figures there were chromosome bridges and fragments, representing double attachment chromosomes. Müntzing concluded that the chromosomes of the two species have homologous segments and that a somewhat different position of these segments in the pairing chromosomes would, by crossing over, cause the bridges and fragments. Various alternative arrangements of the homologous segments could produce bridges and fragments, and fragments might also arise from association of nonhomologous segments at pachytene. These observations demonstrated a mechanism capable of giving rise to chromosomal alterations of evolutionary value.

Two similar investigations on interspecific *Crepis* hybrids have recently been completed. Sherman (1946) studied meiosis in the F_1 hybrids between *C. Kotschyana*, with $n = 4$ chromosomes, and six other species in the same section, 20, all with $n = 5$. Like most other 4-paired species, *C. Kotschyana* lacks the small V-shaped E chromosome which is present in its 5-paired close relatives (figs. 204–214). In all the hybrids chromatin bridges and fragments, similar to those reported by Müntzing, have been found; thus, the existence in the chromosomes of *C. Kotschyana* of certain segments which are homologous with segments in the chromosomes of its 5-paired relatives has been demonstrated. This evidence in itself is a strong indication that the 4-paired *C. Kotschyana* was actually derived from some 5-paired ancestor or ancestors, presumably by a process involving reciprocal translocation. The probable validity of this assumption is greatly enhanced by the results of the following investigation.

Tobgy (1943) studied *Crepis neglecta*, $n = 4$, *C. fuliginosa*, $n = 3$, both F_1 and F_2 hybrids, and certain hybrid forms found in nature. A study of meiosis in F_1 hybrids revealed definite evidence of the existence of homologous segments in the chromosomes of the two species. The A and D chromosomes of *C. neglecta*, through unequal translocation, gave rise to the A and D chromosomes of *C. fuliginosa*; and the B and C chromosomes of *C. neglecta*, through a similar interchange of segments, gave rise to the B chromosome of *C. fuliginosa*. One arm of the C chromosome of *C. neglecta* and its centromere are absent from the complement of *C. fuliginosa*. Hence, it may be inferred that the 3-paired *C. fuliginosa* has been derived from *C. neglecta*, or from a common 4-paired but now extinct ancestor, through a process involving chromosome interchange and resulting in reduction from 4 to 3 pairs of chromosomes, as well as in marked change in karyotype (see p. 9 and fig. 1). Although it must be admitted that the above conclusion is based on indirect evidence, yet this evidence is wholly consistent with the evidence from comparative morphology (see Part II, figs. 255, 257), from the hybrid progeny obtained (see p. 26), and from the geographic distribution of the two species (see Part II, fig. 241).

Since the meiotic irregularities observed in the hybrids discussed above are caused by differences in location of homologous segments in the chromosomes as they existed in the species before they were crossed, the question arises, how did these structural differences in the parental species originate? A general answer to this question is found in the results of the experiments on induced structural changes and on the occurrence of structural changes in the embryos of seeds stored under conditions of high humidity and high temperature. But the question still remains whether structural chromosomal changes *within a species* may give rise to *intraspecific sterility* sufficiently great to permit the accumulation of genic differences between the physiologically isolated races. In other words, do structural chromosomal changes provide a mechanism of intraspecific differentiation?

Gerassimova's achievement.—Karyotypically distinct new forms of *Crepis tectorum*, produced by treating pollen and moist seeds with x-rays, have been investigated by Gerassimova (1939). The main steps in the process of producing these new forms, necessarily omitting many details, are as follows: Two different reciprocal translocations were found among the progeny from x-rayed material. One involved the A and D chromosomes, and the other, the B and C chromosomes. When a strain homozygous for each of the two reciprocal translocations was established, it was found that they were morphologically identical with normal *C. tectorum* and just as self- and cross-fertile. Crossing these two homozygous strains produced F_1 hybrids in which each of the 4 chromosome pairs differed structurally; but the plants resembled normal *C. tectorum* except for their lower fertility. Among the progeny obtained by selfing these hybrids, one, called *C. Nova I*, was homozygous for translocations in all 4 chromosome pairs. In the next generation a plant was found that was homozygous for strikingly different translocations in all 4 pairs; it was called *C. Nova II*. Both of these karyotypically new strains were morphologically identical with normal *C. tectorum* and equally viable and fertile. But, when *C. Nova I* was crossed with normal *C. tectorum*, the F_1 hybrids were only 30 per cent fertile when self-pollinated and slightly more when open-pollinated.

Whatever the precise nature of the sterility of these hybrids may be, there has been created here a highly efficient genetic mechanism, causing isolation between two constant forms of the same species. It is also very probable that crossing over between homologous segments will produce further structural changes causing further sterility. According to Gerassimova, "It becomes inevitable, therefore, that the progeny of the hybrids in question contains a very limited proportion of individuals with intermediate characters, but consists of the two parental types and of individuals which repeat the original hybrid. In other words, there exists a situation characteristic of a hybrid between two genuine species." *C. Nova I* and *C. Nova II* are morphologically indistinguishable from the original *C. tectorum*; but "accumulation of mutational changes should undoubtedly lead in future to such distinction." Although not suggested by Gerassimova, it should be recognized that many or perhaps most of these new mutations, leading to morphological and physiological differentiation, would probably be gene mutations. Furthermore, that sterility of a more complex nature would be built up, along with morphological divergence, by ensuing gene mutations is clearly indicated by the partial intersterility which was shown by Jenkins (1939) to exist between species which differ only in Mendelian variations.

It has now been fully demonstrated that chromosome transformations, similar to those induced by Gerassimova in *C. tectorum*, are produced in considerable numbers in normal dormant seeds when stored under conditions of high humidity and high temperature. They also occur "spontaneously," though more rarely, in seeds stored under ordinary conditions. When one considers the endless variety of conditions under which seeds in nature may await a suitable opportunity for germination, it seems probable that here is an important natural source of this category of genetic evolutionary processes in plants, namely, structural changes in the chromosomes.

THE AMERICAN SPECIES

With the exception of *Crepis nana* and *C. elegans*, which have $n = 7$ chromosomes and belong in section 12, the other members of which are all restricted to Central Asia, all of the native American *Crepis* have the base number, $x = 11$. It was proposed by Babcock and Navashin (1930) and Hollingshead and Babcock (1930) that this group arose as amphidiploid hybrids between Asiatic or extinct American

species with lower chromosome numbers, probably $n = 4$ and 7. This hypothesis has been greatly strengthened by the monographic work of Babcock and Stebbins (1938) and Stebbins and Babcock (1939), supplemented by the research of Stebbins and Jenkins (1939).

Of the ten species recognized, one, *C. runcinata*, has no evident connection with the other nine. This species consists of seven subspecies, all with the same chromosome number ($2n = 22$). It occurs widely in the western United States, the center of its distribution being the central Rocky Mountains. It is definitely mesophytic in its associations; and it is the only American species showing any indications of relationship with the Asiatic species, *C. gymnopus* of Japan and *C. praemorsa* of Eurasia, both of section 13.

The other nine species include seven diploid forms also with the somatic chromosome number $2n = 22$. These diploids are entirely distinct from one another, but they are connected by a continuous, complex series of intergrading, polyploid forms which are partly or wholly apomictic and which have somatic chromosome numbers ranging from 33 to 88. The polyploids are of two sorts: A few are morphological autoploids identical with the diploids except for their *gigas* characteristics; but most of them are allopolyploids which combine the characteristics of two or more diploids. Each of these seven diploid forms is confined to a single whole or part of a climatic province; six occur in northeastern California and adjacent Oregon; and two occur in central Washington, one of which extends into southern British Columbia. The autoploids do not occur outside the province occupied by the corresponding diploid. The allopolyploids show by their distribution the combination through hybridization of the physiological characteristics that determine their distribution. The different forms have different soil preferences, so that their distribution is partly governed by the occurrence of different geological formations; and this is also true of many Old World species.

These species with $x = 11$ were probably not all derived from the same hybrid. Not only does *C. runcinata* stand apart from the other nine; but, among the latter, three distinct subgroups must be recognized (see Part II, p. 572). And even among these subgroups there are strong individual specific differences. In fact, the Asiatic species which show the strongest resemblances to these American species are found in six other sections (see p. 69). Thus, several different hybrids must have been involved in the origin of these species and, since no evidence exists that any of the hybrids ever reached North America, it is probable that they occurred in Asia. After the amphidiploids reached North America two processes began. First, they hybridized to produce more or less sterile progeny, and at the same time they may have produced autoploid offspring. Second, by means of chromosome doubling in the diploid ($2n = 22$) F_1 hybrids, or by hybridization of autoploids of two different species, or between the autoploid of one species and the diploid of another, the various intermediate allopolyploids were produced. The subsequent evolution of the species in this section has been determined by hybridization, polyploidy, and apomixis, coupled with the selective effects of the environment.

GENETIC EVOLUTIONARY PROCESSES IN CREPIS

The subject of genetic evolutionary processes in *Crepis* has been discussed at some length by Babcock (1942) and by Babcock, Stebbins, and Jenkins (1942). But it seems appropriate to conclude this review of the research on *Crepis* having a bearing on systematics with a brief summary of the conclusions reached concerning the genetic processes which have been responsible for evolution in this genus.

Primary changes.—The genetic processes primarily causing evolution in *Crepis*

are gene mutations (see p. 12) and structural changes in the chromosomes leading to intraspecific sterility and karyotype evolution.

Gene mutations.—Two different aspects of *Crepis* evolution are found to depend upon gene mutations, namely, morphological and physiological differentiation, and accumulation of intra- and interspecific sterility; a third, reduction in chromosome size, may also be attributed to gene mutations.

1) Differentiation.—There are numerous polymorphic species of *Crepis*, for example, *C. capillaris*, *C. tectorum*, *C. Dioscordis*, and *C. foetida*, in which genetic experiments have shown that intraspecific variations, both morphological and physiological, are Mendelian in their inheritance. There are also groups of very close species with identical karyotypes between which numerous Mendelian differences exist, for example, the group of insular endemics investigated by Jenkins (1939) and *C. foetida* and its two close relatives, *C. eritreensis* and *C. Thomsonii* (Babcock and Cave, 1938). There can be no doubt that gene mutations have made possible the gradual accumulation of differentiating Mendelian variations in such species. Furthermore, this process of gene mutation is always going on and is ready to play its part whenever circumstances favor differentiation and discontinuity. When intraspecific isolation is accomplished through changes in chromosome structure, gene mutations will continue the process of differentiation.

2) Accumulation of intersterility.—In addition to Jenkins' insular endemics discussed above (p. 17), other evidence from *Crepis* exists showing that gene mutations cause the accumulation of intersterility in isolated populations. In the *C. foetida* group mentioned above, some of the first hybrids studied were highly fertile, whereas others were more or less sterile. It is safe to assume, therefore, that the interfertility relations among the species of this group is comparable to that found in the insular endemics. Then, we also have the evidence from intraspecific hybrids in *C. capillaris* and *C. tectorum* mentioned above. Although evidence is lacking on the regularity of meiosis in these two hybrids, their lowered fertility is probably due mainly to genic differences between the crossed strains.

3) Reduction in chromosome size.—The parallelism between the general trend toward reduction in chromosome size and progressive reduction in the plants and the length of their life cycles throughout this genus was mentioned above (p. 12). This parallelism in evolutionary trends was first mentioned by Babcock and Cameron (1934), without assumptions being made regarding its possible cause. Although no direct evidence regarding the cause of chromosome shortening is yet available in *Crepis*, plenty of evidence shows that the morphological and physiological variations in the plants depend on genic differences. Nor does evidence exist that such structural changes in the chromosomes as reciprocal translocations cause any somatic changes. This was pointed out in Gerassimova's translocant strains of *C. tectorum* (p. 22). Hence, the progressive reduction in size and length of life cycle so prevalent in *Crepis* must be attributed to the accumulation of gene mutations. It would seem reasonable, therefore, to assume that this trend in reduction in chromosome size is also a visible effect of genotypic changes. The contention that loss of large segments of euchromatin is the cause of general reduction in chromosome size is, of course, not to be considered because of the known deleterious effects of such losses. The loss of segments of heterochromatin may, in some instances, have caused reduction in length. This certainly is true of *C. fuliginosa*. As stated above (p. 21), this is the species which lacks parts of the C chromosome of *C. neglecta*, including the centromere, which parts, Tobgy (1943) points out, are largely composed of heterochromatin. That this sort of change is the chief cause of chromosome shortening, however, seems unlikely. This problem is discussed

further by Babcock, Stebbins, and Jenkins (1942, pp. 358-359) and Babcock and Jenkins (1943, pp. 271-272). Although it is impossible as yet to determine the exact nature of the genetic control of chromosome size, nevertheless, the fact of some genetic control of chromosome size is clearly indicated. Furthermore, the progressive reduction in the chromosomes, which has accompanied reduction in size and life cycle of the plants, may well depend upon gene mutations.

Structural changes in the chromosomes.—Changes in chromosome structure have been shown by the evidence reviewed above to have played two different roles, namely, the genesis of interspecific sterility and progressive differentiation in the karyotype. The relative importance of these roles in the origin of species is clearly indicated by the evidence from *Crepis*.

1) Genesis of intersterility leading to speciation.—The origin of intersterility within a species through changes in chromosome structure was beautifully demonstrated by Miss Gerassimova (1939). On *a priori* grounds this is the only role played by changes in chromosome structure which could be of primary importance in speciation. And, since the origin of such sterility might either precede or follow extensive differentiation through the accumulation of gene mutations, the one process, as a cause of speciation, cannot be considered any more basic than the other. This conception is advanced, however, with the one reservation that there is evidence from *Crepis* indicating that certain genetic differences among the individuals of a species have a marked effect on the frequency of occurrence of chromosome changes caused by x-rays. Levitsky (1937) reported that the chromosomes in *C. capillaris* are very stable, but that among 295 plants grown from x-rayed seeds, there were 25 showing deviations in chromosome morphology. These were confined to 11 out of 28 families and just 2 of these families had 11 of the 25 cases. Hence, he concludes, there are genetic differences conditioning structural instability and these may be an important cause of karyotype evolution. If future investigations should prove the existence of genes which condition liability to the occurrence of structural changes, then, to this extent, gene mutations would have to be considered a more basic process than gross chromosomal changes. For the present, however, both gene mutations and structural changes leading to karyotype evolution must be recognized as of primary importance, at least in plants.

2) Karyotype evolution.—Karyotype evolution in *Crepis* is characterized by progressive reduction in chromosome number, increase in asymmetry of the individual chromosomes, and reduction in total length of the chromosomes. (1) That the parallelism between reduction in chromosome number and reduction and specialization in the plants is coincidental should be emphasized. Evidence has been presented showing that reduction in chromosome number has been made possible by changes in chromosome structure, principally by reciprocal translocations; whereas progressive reduction and specialization of the plants has depended entirely upon gene mutations. Gene mutations and reciprocal translocations between chromosomes proceed independently but apparently fortuitously in *Crepis*, except so far as the latter may depend upon the former. (2) The parallelism between increase in asymmetry of the individual chromosomes and progressive evolution of the species is likewise apparently fortuitous. Modification of the individual chromosomes, like reduction in chromosome number, depends on such changes in chromosome structure as reciprocal translocation; whereas morphological and physiological differentiation within and between species depends on gene mutations. (3) Reduction in chromosome size, on the other hand, and reduction in the plants can logically be referred to the effects of gene mutations. This particular parallelism appears not unlikely to rest upon a common cause for both categories of phenomena.

Secondary changes.—The genetic processes involved secondarily in the evolution of *Crepis* are interspecific hybridization, polyploidy, and apomixis.

Interspecific hybridization.—The roles of interspecific hybridization are: (1) the origin of a small number of new species; and (2) the augmentation of karyotype evolution.

1) Origin of new species.—Although the evidence is necessarily all indirect, it appears practically certain that the ten previously discussed American species of *Crepis*, with the base number $x = 11$, provide convincing evidence that interspecific hybridization has been primarily responsible for a small but very distinct group of species now situated on the extreme periphery of the range of the genus. The seven species in section 12, *Ixeridopsis* (see Part II, pp. 528-547), and the five species in section 18, *Pyrimachos* (see Part II, pp. 632-648), may have originated through hybridization between certain ancestral species of *Crepis* and either *Ixeris* or *Youngia*. If the assumption of hybrid origin is true of all of these three groups, this accounts for only 11 per cent of the species in the genus.

2) Augmentation of karyotype evolution.—In Tobgy's (1943) research on *C. fuliginosa* \times *C. neglecta*, one of the F_2 segregants was similar in morphology and karyotype to a certain plant grown from seeds collected in the wild by Miss S. P. Topali in northeastern Thessaly, where it is known that the two species have come into contact. This particular form is about 70 per cent fertile. Its karyotype appears like that of *C. neglecta*, but one or more chromosomes contain segments from *C. fuliginosa*, which explains the presence of certain characters from that species. The occurrence of a duplicate of this wild form among Tobgy's F_2 segregants provides a clue to one method of the origin of intergrades occurring in nature. It also indicates that interspecific hybridization may operate as a secondary process in the origin of species through interspecific translocations leading to entirely new types of plants with new types of chromosomes.

Polyplody and apomixis.—As is shown by the fact that comparatively few species exhibit either polyploidy or apomixis, both these phenomena are of secondary importance in the evolution of *Crepis*.

1) Polyploidy.—Among the rare polyploids that have been discovered in this genus, four have been so little studied that their classification as auto- or allopolyploid is purely conjectural. These are *C. polytricha* (Part II, p. 266), *C. incana* (Part II, p. 480), *C. taygetica* (Part II, p. 482), and *C. ciliata* (Part II, p. 433). The last-named species is certainly an octoploid, and, like *C. biennis*, it may be a doubled-up amphidiploid which arose from hybridization between two 5-paired species. In the complex polymorphic species, *C. vesicaria*, three of the subspecies, namely, *typica*, *taraxacifolia*, and *myriocephala*, are mostly diploid, but natural tetraploid forms occur which from their morphology certainly appear to be autoploids. But subsp. *stellata* appears on the same grounds to be an amphidiploid (or rather a mixture of amphidiploid forms and variants derived from them) originating from a cross or crosses between two other subspecies. Another tetraploid species, *C. crocea* (first reported by Hollingshead and Babcock, 1930, as *C. Bungei*, no. 2174), appears to be an amphidiploid derived from a hybrid between *C. Bungei* and *C. oreades* (see Part II, p. 504). In all but two of the native American species of *Crepis*, as was explained above, polyploidy has played an important role in differentiation and extension of the ranges. A similar situation seems to exist in the group of five species comprising section 18, *Pyrimachos*, of southeastern Asia. But in these the evidence rests entirely on morphological evidence, especially of the pollen grains.

2) Apomixis.—In all but one (*C. runcinata*) of the American species with the base number $x = 11$, apomixis has operated, along with polyploidy, to cause still greater

differentiation within this group. But the various intergrading complexes are not equally likely to persist. In some of them the diploid ($2n = 22$) form is dominant and aggressive in most parts of its range; whereas in other complexes the diploid is restricted in distribution. The latter type of species is destined eventually to become extinct. The ultimate fate of an agamic complex, of which the sexual ancestors have become restricted or extinct, can be predicted; it will persist so long as conditions remain favorable, but it will be unable to meet new changes in the environment and, therefore, will in time become more and more restricted and will eventually die out. As Stebbins (1941) concludes, apomixis is not a major factor in evolution, however important it may be in increasing the polymorphism and geographic distribution of the genera in which it is found.

In this connection it should be pointed out that the review by Huxley (1943) of the monograph on the American species of *Crepis* (Babcock and Stebbins, 1938) gives an unfortunate impression concerning the *evolution of the genus as a whole*. The statement: "we are given a very interesting picture of the varying roles of selection, environment and polyploidy in a facultatively apomictic plant genus" certainly does convey the idea that apomictic reproduction is common throughout the genus, whereas just the opposite is true. Polyploidy and apomixis play a relatively unimportant part in the evolution of the genus as a whole, no matter how important they have been in the differentiation and ultimate fate of nine of the native American species. And the only other group of *Crepis* species in which polyploidy and apomixis appear to have been of much importance is the group of five species comprising the section Pyrimachos of southeastern Asia. It is only fair to add, however, that the general reviews of the evidence on *Crepis* as a whole (Babcock, 1942; Babcock, Stebbins, and Jenkins, 1942) probably were not available to Huxley before the publication of his important book.

Finally, it should be noted that, although most of the *Crepis* apomicts are of hybrid origin (allopolyploids), yet hybridization is probably an accompanying phenomenon rather than the cause of apomixis. The presence of predominantly apomictic reproduction, together with the occasional production of hybrid and segregating types by means of the sexual process, accounts very well for the variability of these species.

SUMMARY

Two decades of research by numerous persons on various species and hybrids of *Crepis* have produced results of considerable significance for the problems of systematics in this genus. These results may be summarized as follows:

1) Comparative morphology provides the primary basis for inter- and intra-specific classification in the Crepidinae. But in *Crepis*, at least, the evidence from comparative karyology, genetics, and cytogenetics has proved to be of the greatest value in determining phylogenetic relations and thus in approximating a truly natural classification. The morphological criteria of relationship are discussed in chapter 3.

2) Chromosome number and morphology are both important in relation to phylogeny in *Crepis*. Of the 113 species studied cytologically, 97 are characteristically diploid species (in a few of them tetraploid variants sometimes occur, but even in these species, most of the plants are diploid). The other 16 comprise 10 American and 6 Eurasian polyploids. Among the 80 or more species which have not been studied cytologically, only the 5 species comprising section 18 give a strong indication of being highly polyploid. Thus, in the evolution of the genus as a whole, polyploidy has been of relatively slight importance, and apomixis is of still less significance.

Of the 97 known diploid species, all but 3 have either 3, 4, 5, or 6 pairs of chromosomes. The other 3 have 7 pairs, but, as was explained (p. 5), these require a special hypothesis concerning their origin. On morphological grounds the most primitive species have 6 and 5 pairs of chromosomes, and the most advanced species, 4 and 3 pairs. Furthermore, a definite parallelism exists between karyotype evolution in *Crepis* and progressive morphological reduction and specialization in the plants. This parallelism between the chromosomes and the plant morphology provides an unusually strong basis for the phylogenetic relations shown by the sequence of the sections in Part II. See also chapter 4.

3) Cytogenetic research has still further strengthened the evidence on phylogenetic relations in this genus by demonstrating the method by which reduction in chromosome number takes place (cf. Tobgy, 1943, p. 107). Of less significance in phylogeny, but of equal importance in evolution, is the demonstration by Miss Gerassimova (p. 22) that structural changes in the chromosomes may initiate differentiation within a species by creating intrsterile groups within it. Another important contribution of cytogenetics is the aid it has given in working out the especially difficult complexes of intergrading forms, which comprise most of the American species of *Crepis*, and the aid it has given in the phylogenetic treatment of this group.

4) Genetic investigations have shown that a few gene mutations may be responsible for morphological differences—receptacular paleae, for instance, which were previously used by taxonomists in defining generic limits. It has also been shown that gene mutations may be responsible for the accumulation of interspecific sterility, so that geographically isolated entities which are now partly intersterile may be expected to become more so in course of time, a consideration to be given due weight in delimiting species. Finally, the data which have been accumulated on interspecific hybrids in *Crepis* have been found to agree very well with the sectional classification arrived at primarily on morphological grounds (see chapter 3).

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CHAPTER 2

TAXONOMIC CONCEPTS

INTRODUCTION

ONE OF THE chief aims of the present author has been to convince others of the fundamental importance of a truly scientific taxonomy, that is, a taxonomy which rests upon the broadest possible foundation of biological disciplines. For only in this way will taxonomy come to occupy the fundamental place which it deserves in the realm of natural science or become "the focal point of biology" (Turrill, 1942, p. 690), and only in this way will biology in general come to rest upon the surest foundation. It therefore becomes necessary for any biologist, who wishes to understand the relations of taxonomy to his own field of work, to consider along with the taxonomist the basic concepts used in present-day systematics.

Since the eighteenth century it has been generally recognized among systematists that the basic concepts with which they must deal are those of genus and species. But the question whether those two terms denote nothing more than concepts or whether the specific and generic names applied to plants and animals designate real entities in nature is one on which there still exists diversity of opinion (Anderson, 1940; Camp and Gilly, 1943).

It appears that this diversity of opinion regarding the reality or nonreality of clearly recognizable smaller and larger groups of organisms is largely due to the difficulties in clearly distinguishing between the actual groups. These obstacles arise, it must be admitted, because Nature finds plenty of ways by which to make difficult the clear and complete delimitation of such natural groups. Nevertheless, early man became aware of the existence of genera of animals and plants. That the recognition of genera has actually been going on since or before the dawn of history is interestingly shown in the following quotation from Bartlett (1940) :

Classical botany was folk science. It did not progress far beyond the gathering together of folk beliefs and practical information. Theophrastus dealt almost entirely with cultivated plants, and Dioscorides with medicinal ones, and each systematized the knowledge or belief of his time with regard to the particular plants that interested him. Although they had no Dioscorides to record it, the illiterate barbarians of northern Europe probably had a folk science and terminology nearly as extensive and useful as that of Greece or Italy. Contemporaneously, an equivalent folk science would have been in Egypt, in Ethiopia, in Palestine, in Persia, in Mesopotamia. There is, as a matter of fact, a modern interpretation of an old Babylonian herbal. China has its ancient knowledge of plants with a surviving literary record in a long series of printed pêngs'ao or herbals dating back at least to 1100, and based upon folk science hundreds or thousands of years older. China passed its learning on to Japan, where there was certainly already a native lore which was grafted upon the Chinese. India early had symptoms of native medicine and associated plant lore which have come down to the present time partly by way of literature and partly by way of tradition. Anyone who delves into the beliefs of the peoples of the East Indies cannot fail to be impressed by the voluminous lore of plants, comparable in extent and value to that of the classical Greeks or Romans, and maintained by a nomenclature quite as scientific as the best in European botany during the time preceding Linnaeus. The New World had developed its own plant lore, an extensive body indeed in ancient Mexico, with its associated system of plant names and plant classification. Wherever we look into the matter, whatever the people or the language, we find naming and classification of plants, and almost invariably a more or less well-defined idea of the genus, as the smallest group that almost everyone might be expected to have the name for in his vocabulary. It might or might not be subdivided into species.

The idea that the generic concept is a characteristic of folk science will be found carefully developed in E. L. Greene's *Landmarks of Botanical History*. I have carried the development somewhat farther, anxious to show that the generic idea is concerned in its beginnings with the psychology of language, that these beginnings are lost in pre-history, and that we can only recover some conception of them by the consideration and comparative study of the plant names of people everywhere.

Another important reason for persistence of the confusion of thought concerning the reality or nonreality of species and genera is the practice of pigeonholing. The inadequacies of equipment and personnel in museums and herbaria throughout the world may be partly responsible for this practice. But unfortunately what might be condoned as a temporary expedient in filing specimens seems to have profoundly affected the thinking of many biologists. For, along with this practice, two tendencies have developed on the part of taxonomists: Some err to an extreme in the "lumping" of both species and genera, whereas others go to an extreme in the "splitting" of those same groups into segregates. All too often this lumping or splitting of truly natural groups has been based on purely artificial criteria. What, then, shall be recognized as the soundest criteria for the recognition of genera and species? The answer has been given in unmistakable terms by Hall and Clements (1923, p. 6) in the following paragraph on *the nature of the genus*.

In the prevalent view the genus appears to be regarded merely as a concept, and it is often stated that it does not actually exist in nature. This is doubtless true for those who regard the genus merely as a pigeon-hole, chiefly convenient for the filing of new species. Such a view has its justification in the usual practice of making genera, and especially in the recent flood of generic segregation. It is not supported by the evidence drawn from the methods of evolution or the record of phylogeny. To the student of evolution, the genus represents a certain characteristic portion of the line or field of specialization, and its existence is as definite as that of the species which constitute it. It may be more difficult to recognize, but this is primarily the fault of outlook and method. In the absence of definite criteria, the chief difficulty centers about the rank and limits of genera. As a consequence of the unrestricted play of personal opinion, not infrequently aided by bias or carelessness, present-day taxonomy contains genera of every possible quality. Many of these disappear completely when the test of evolution is applied to them. Given the family, genus, and species as major units, these will regularly be differentiated into tribes, sections, and variads, respectively. This is a necessary corollary of the principle that the processes of evolution are constantly and universally at work. The basic laws of conservation of energy and material, division of labor, and increase of parental care lead inevitably to divergence, and hence to the splitting of the generic stock into sections, and of the specific stock into variads.

That man's awareness of *species* has been a fundamental factor in his evolution and survival is emphasized by Camp and Gilly (1943, pp. 380-381):

There are even some among us who have advocated that we discard the concept of species altogether. Therefore, the question which the systematist should seek first to answer is not: Upon what criteria should the concept of the species-unit be based? Rather, he must enquire: Does the species-unit deserve to be a fundamental philosophical concept? This, perhaps fortunately for his own peace of mind, has long ago been decided for him.

The concept of species or *kind*, as a unit, has become so firmly entrenched in the mind of man—so much a part of his awareness, so necessary to his basic philosophy—that it remains only for the systematist to interpret this unit and give to it (1) a circumscription which is not only biologically as sound as possible, but (2) which also is in accord with an effective system of nomenclature. Furthermore, the interpretation of these items must be balanced; there must be no undue emphasis of one above the other, otherwise a bifurcation of concept will result leading to chaos in systematics. These two criteria—practical expedience in the interpretation of biological phenomena, and the application of an effective system of nomenclature—are the elements from which the systematist must fashion his concept of species.

In summarizing this brief introduction two thoughts need to be emphasized. First, many specific and generic groups of plants and animals have been recognized by man since time immemorial. Since these groups are objective realities, it may be assumed that all organisms may be classified into truly natural groups, provided that adequate criteria can be found for such classification. This, of course, is where the trouble begins; but because an achievement is difficult is no excuse for failing to attempt it. Second, the only criteria which can safely be used in establishing a natural classification of individuals into species and of species into genera are those which represent or reflect the evolution of those species and genera.

THE GENUS CREPIS

A review of the taxonomic history of *Crepis* (see Part II) reveals a continual swinging to and fro between lumping and splitting. This was caused largely by the lack of any fundamental guiding principle as a basis for classification. When the problem was taken up by the present author there were many species masquerading under the name *Crepis* which belonged in other genera. In many it was not difficult to show good reasons for their exclusion. For example, there are several South American and Mexican species of *Hieracium* with attenuate achenes and white pappus which had been described as *Crepis*. But it was found that in their other characteristics they were more like *Hieracium*; and when some of them were examined cytologically (for example, *H. Fendleri* = *C. ambigua* A. Gray) it was found that they have 8 or 9 pairs of chromosomes, like those of other species of *Hieracium*. A similar situation holds with other species representing *Lactuca*, *Ixeris*, *Launaea*, *Aethorrrhiza*, *Tolpis*, *Taraxacum*, and *Troximon*, not to mention several genera characterized by plumose pappus.

After such delimitation there still remained three groups of species which had long been accepted in *Crepis* and which were morphologically closer to *Crepis* than the genera mentioned above. But the cytological evidence, so far as the chromosomes had been examined, indicated that they were distinct phylogenetic groups. The cytological evidence on these and other related genera in the Crepidinae was reported later by Babcock, Stebbins, and Jenkins (1937). It was at this time that Dr. G. L. Stebbins, Jr., became associated with the author and undertook a general survey of all the genera in the tribe Cichorieae, giving special attention to the sub-tribe Crepidinae.

As a result of this survey, decisions concerning the three difficult groups mentioned above could be reached with considerably more assurance. The most important of these, phylogenetically, is the genus *Dubyaea* DC. As reconstituted by Stebbins (1940), this includes *Crepis bhotanica* Hutchinson (= *C. Dubya* Marq. et Shaw), *C. (Paleya) oligocephala* Sch. Bip., and *C. tsarongensis* Anthony, along with several other species which were not previously assigned to *Crepis*. The 9 species comprising this genus are all endemic in the Sino-Himalayan region. They are believed to be the living representatives of a larger group of species from which many of the genera in the subtribe Crepidinae originated. In the present author's opinion this genus had its origin in north Central Asia or farther to the east in northern Asia. This matter is discussed more fully in chapters 5 and 6. Another group of species, with a distribution resembling that of *Dubyaea*, had been referred to in the literature as the Glomeratae and had been recognized as showing affinity with *Prenanthes*. In fact, they had all been originally published as either *Crepis* or *Prenanthes*. This group became a new genus, *Soroseris* (Stebbins, 1940). Meanwhile, the third and most troublesome group of species had been disposed of by reviving the genus *Youngia* DC. and referring to it 19 species which had been originally described as *Crepis* (cf. Babcock and Stebbins, 1937). The reasons for the separation of all these species from *Crepis* are fully explained in the references cited. After all this work of delimitation, the net result is the assemblage of the 196 species included in this monograph. It is the author's firm belief that, with the exception of two small sections (12 and 18), they comprise a monophyletic group. Furthermore, these two sections (12 and 18) should, on morphological grounds, be included, even though they may have originated through hybridization between primitive *Crepis* species and species which became the ancestors of groups now recognized as different genera.

THE KINDS OF SPECIES FOUND IN CREPIS

The species concept has been one of the most controversial subjects of biological literature since the time of Darwin. In the present brief discussion, reference is made to only two of the earlier contributions which influenced my own views of this problem. Early in the present century Poulton (1908, pp. 46-94) published his illuminating essay, "What Is a Species," in which he reviewed the ideas of many of the older naturalists and set up several criteria that might be used in formulating a species concept. Robson (1928) presented a well-rounded discussion of the subject, with emphasis on physiological differentiation, distribution, isolation, and on correlation and the origin of groups. With these contributions as a basis, the present author (1931) formulated the following ideas as essential for a working concept of species:

- 1) Common structural characteristics which unite certain individual organisms into one group, and a common genetic basis for the group represented by a specific chromosome complement.
- 2) Characteristic features which distinguish such entities from one another, one of these features frequently being the chromosome complement.
- 3) Relative stability combined with more or less variability within the group. This stability is made possible by a high degree of regularity in chromosome distribution from cell to cell and from parent to offspring, while inherited variations arise from occasional changes of one sort or another in the chromosomes.
- 4) Common descent of all individuals of the group from one or more preexisting species is made possible by the known mechanism of heredity and genetic variation.
- 5) Syngamy or free intercrossing and high interfertility among the individuals of the group are just what would be expected in organisms in which almost all of the genes in all of the chromosomes are homologous.
- 6) Absence of free intercrossing and usually high, if not complete, sterility in hybrids between different species (with a few exceptions) are logical results of the accumulation of genic and larger chromosomal differences between diverging groups of individuals within a species.
- 7) The existence in many species of subspecific groups, occupying different but usually overlapping geographic areas. These subspecies differ more from one another in structure and interfertility or both than do the individuals composing each subspecies, but the subspecies are sometimes still connected with one another by intergrading forms. This is the necessary result of genetic variability within the species, plus the influence of environmental variability, isolation, and natural selection or random fixation. It is a stage in one process of species formation.

The necessity of including the seventh item arises from the fact that some species are polymorphic, while others are not. It is for just such reasons that, up to the present, no fully adequate and satisfactory definition of the term species has been forthcoming (Mayr, 1942, p. 147). Although Hogben's assertion that "The word 'species' has no single meaning" (Hogben, *in Huxley*, 1940) is true; yet a concept of species sufficiently clear and definite for purposes of the present discussion can be stated briefly. Several such statements have been published, for example, that of Mayr (1942, p. 120), who says: "Species are groups of actually or potentially interbreeding populations which are reproductively isolated from other such groups." It should be noted, however, that a species may consist of a *single* population of individuals. In short, a species is a single population or a series of populations of individual organisms; and, just as no two single individuals are just alike, so, no two populations of individuals are identical. Just as no single all-inclusive definition of species has been found, so, no single criterion for distinguishing between species has been agreed upon. Because of the endless differences in degree of differentiation within the individual organism, ranging from that of the simplest to the most complex, decisions concerning just how much difference between populations shall be sufficient for the recognition of a new species had best be left to the judgment of biosystematists who specialize in the various fields of organic life.

Fundamental to the recognition of kinds or types of species among the flowering plants is the fact that species are perpetuated by the reproduction of individuals and that the possible methods of reproduction are definitely limited. This important fact sets up conditions making for resemblances and differences between species. Furthermore, each species originates, perpetuates itself for a limited period, and disappears. At different stages in its life history it will present very different aspects according to its success in competing with other organisms and with the inanimate environment. Thus, the method of reproduction and the stage of development of a species are two factors which determine the aspect of a species at a given time.

Another important factor in determining kinds of species is the type of genetic system which operates in the perpetuation of the species. This depends on many other things in addition to the method of reproduction. If the method of reproduction is sexual, then the fertility relations between the individuals or between intra-specific groups will certainly affect the type of the population. The chromosome situation in the species is another important genetic factor affecting type of population, since the individuals may be diploid, polyploid, allopolyploid, euploid, or dysploid, or a mixture of two or more of these conditions.

Based on such considerations as the foregoing, Camp and Gilly (1943) have introduced a clearly defined series of categories of species, under which it is possible to classify at least provisionally all the species of *Crepis*. But until more information is available, the classification of many of the species under these categories must remain only tentative. Accordingly, the simple scheme of classification shown in table 1 is presented mainly for the purpose of giving a picture of the nature of the species populations existing in this genus. In addition, classification according to Camp and Gilly's categories is incorporated into this representation by the capital letter or letters following each species. When the classification is tentative or doubtful, which is often true, the letter is followed by a question mark. The section in which each species belongs is shown by the number preceding it. The definitions of such of Camp and Gilly's categories as apply to *Crepis* and the letters designating them are as follows:

Homogeneon: a species which is genetically and morphologically homogeneous, all members being interfertile (H).

Parageneon: a species with relatively little morphological or genetical variation throughout its range, but which contains some aberrant genotypes; all its individuals are interfertile (P).

Rheogameon: a species composed of segments of reasonably marked morphological divergence the distributions of which are such that gene interchange may take place in sequence between them; individuals of contiguous segments are interfertile (R).

Dysploidion: a species composed of morphologically similar members of a dysploid series (for example, 10, 11, 12, 13, ...) the individuals of which are sexually reproductive (D).

Euploidion: a species the individuals of which are sexually reproductive and which is composed of segments with a common origin arranged in a euploid series (such as 8, 16, ...); the segments are morphologically separable and, although similar in appearance, because of differential responses in various environments, seem to intergrade (E).

Alloploidion: a species derived by allopolyploidy; its individuals, although usually highly variable, are interfertile (A).

Apogameon: a species containing both apomictic and nonapomictic individuals (Ap).

From the rare occurrence of the index letters D, E, and A in table 1, it will be obvious that almost all *Crepis* species are believed to consist entirely of diploid individuals. But at the same time, it must be noted that occasional aberrant individuals with slight deviations from the diploid number of the species are liable to be found in any species. These, however, have little if any permanent effect on the genetic system of the species. Inability to classify a species definitely in one of Camp and Gilly's categories is, of course, due to lack of definite information. The actual

TABLE 1

CLASSIFICATION OF 196 SPECIES OF *CREPIS* IN ACCORDANCE WITH METHOD OF REPRODUCTION AND
DEGREE OF COMPLEXITY
(Each species is preceded by its section number)

REPRODUCTION SEXUAL SO FAR AS KNOWN — MONOMORPHIC SPECIES
Known at present from only one or very few stations

1	<i>C geracioides</i>	P ?	10	<i>C khorassanica</i>	H ?
4	<i>C albiflora</i>	H ?	10	<i>C taygetica</i>	H ?
4	<i>C dioritica</i>	P ?	10	<i>C Guioliana</i>	H ?
5	<i>C willemetioides</i>	H ?	10	<i>C crocifolia</i>	H ?
8	<i>C kilimandscharica</i>	H ?	10	<i>C athoa</i>	H ?
8	<i>C keniensis</i>	H ?	11	<i>C Schachtii</i>	H ?
8	<i>C suffruticosa</i>	H ?	11	<i>C Faurehana</i>	H ?
8	<i>C iringensis</i>	H ?	11	<i>C demavendii</i>	H ?
8	<i>C cameroonica</i>	H ?	12	<i>C alaica</i>	H ?
8	<i>C urundica</i>	H ?	12	<i>C naniforma</i>	H ?
8	<i>C chirindica</i>	H ?	14	<i>C irtutensis</i>	P ?
8	<i>C congoensis</i>	H ?	16	<i>C connexa</i>	H ?
8	<i>C caudicalis</i>	H ?	16	<i>C elbrusensis</i>	H ?
8	<i>C glandulosissima</i>	H ?	19	<i>C amanica</i>	H ?
8	<i>C ugandensis</i>	H ?	20	<i>C eritreensis</i>	H ?
8	<i>C simulans</i>	H ?	20	<i>C tybakiensis</i>	H ?
8	<i>C Gossweileri</i>	H ?	21	<i>C Gmelini</i>	H ?
8	<i>C Friesii</i>	H ?	24	<i>C insignis</i>	H ?
8	<i>C Mildbraedii</i>	H ?	25	<i>C Fontiana</i>	P ?
8	<i>C Bruceae</i>	H ?	25	<i>C canariensis</i>	P ?
10	<i>C Strausii</i>	H ?	25	<i>C Balliana</i>	II ?
10	<i>C darvasica</i>	H ?	25	<i>C Claryi</i>	H ?
10	<i>C ciliata</i>	P ?	26	<i>C atheniensis</i>	H ?
10	<i>C bertiscea</i>	H ?	26	<i>C Muhlissii</i>	H ?
10	<i>C albanica</i>	H ?	27	<i>C Forskali</i>	H ?
10	<i>C dens-leonis</i>	H ?	27	<i>C filiformis</i>	H ?

Known from several or many stations

1	<i>C viscidula</i>	H ?	11	<i>C Robertioides</i>	P ?
2	<i>C kashmirica</i>	P ?	11	<i>C abyssinica</i>	H ?
4	<i>C terglouensis</i>	P ?	12	<i>C corniculata</i>	P ?
4	<i>C rhaetica</i>	P ?	12	<i>C lactea</i>	H ?
4	<i>C hokkaidoensis</i>	H ?	12	<i>C elegans</i>	P ?
4	<i>C polytricha</i>	P ?	13	<i>C gymnopus</i>	H ?
5	<i>C lapsanoides</i>	P ?	13	<i>C praemorsa</i>	P ?
5	<i>C lyrata</i>	P ?	14	<i>C Bungei</i>	P ?
5	<i>C hierosolymitana</i>	P ?	16	<i>C sahendi</i>	P ?
6	<i>C pontana</i>	P ?	17	<i>C napifera</i>	P ?
8	<i>C Schultzei</i>	H ?	19	<i>C Stojanovi</i>	P ?
8.	<i>C subscaposa</i>	P ?	19	<i>C pterothecoides</i>	P ?
10	<i>C songorica</i>	P ?	20	<i>C syriaca</i>	D, P ?
10.	<i>C chondrilloides</i>	P ?	20	<i>C Schimperi</i>	H ?
10	<i>C auriculaefolia</i>	P ?	21	<i>C elongata</i>	H ?
10	<i>C Baldacchii</i>	H ?	23	<i>C patula</i>	P ?
10	<i>C Pantocsekii</i>	H ?	23	<i>C Zacynthia</i>	P ?
10.	<i>C Sibthorpiana</i>	H ?	24	<i>C cretica</i>	P ?
10	<i>C incana</i>	P ?	24	<i>C apula</i>	H ?
11	<i>C pinnatifida</i>	H ?	24	<i>C Suffreniana</i>	P ?
11.	<i>C bithynica</i>	P ?	25	<i>C spathulata</i>	H ?
11.	<i>C tenerrima</i>	H ?	25	<i>C Clausonis</i>	P ?
11.	<i>C xylorrhiza</i>	H ?	25	<i>C Noronhaea</i>	P ?
11.	<i>C Hookeriana</i>	P ?	25	<i>C libyca</i>	P ?

TABLE 1—(Continued)

REPRODUCTION SEXUAL SO FAR AS KNOWN.—POLYMORPHIC SPECIES
One or more minor variants recognized

1. <i>C. sibirica</i>	P ?	12. <i>C. flexuosa</i>	P ?
1. <i>C. paludosa</i>	P ?	13. <i>C. incarnata</i>	P ?
4. <i>C. Jacquinii</i>	P ?	14. <i>C. tectorum</i>	P
4. <i>C. chrysanthia</i>	P ?	16. <i>C. purpurea</i>	P ?
5. <i>C. smyrnaea</i>	P ?	16. <i>C. frigida</i>	P ?
5. <i>C. mollis</i>	P ?	19. <i>C. palaestina</i>	P
5. <i>C. montana</i>	P ?	20. <i>C. alpina</i>	P ?
5. <i>C. Mungierii</i>	P	20. <i>C. rubra</i>	P
6. <i>C. conyzaeifolia</i>	P ?	20. <i>C. Kotschyana</i>	P
6. <i>C. blattarioides</i>	P ?	20. <i>C. Thomsonii</i>	P ?
7. <i>C. achyrophoroides</i>	P ?	21. <i>C. tibetica</i>	P ?
7. <i>C. elymaitica</i>	P ?	23. <i>C. multiflora</i>	P
8. <i>C. alpestris</i>	P ?	24. <i>C. nicacensis</i>	P
8. <i>C. meruensis</i>	P ?	24. <i>C. capillaris</i>	P, E ?
8. <i>C. carbonaria</i>	P ?	24. <i>C. parviflora</i>	P
8. <i>C. Ellenbeckii</i>	P ?	24. <i>C. neglecta</i>	P
8. <i>C. Swynnertonii</i>	P ?	24. <i>C. corymbosa</i>	P ?
9. <i>C. tingitana</i>	P ?	24. <i>C. fuliginosa</i>	P
9. <i>C. leontodontoides</i>	P	25. <i>C. Salzmannii</i>	P ?
10. <i>C. sonchifolia</i>	P ?	25. <i>C. Bourgeau</i>	P ?
10. <i>C. biennis</i>	P, A ?	25. <i>C. divaricata</i>	P ?
10. <i>C. pannonica</i>	P ?	25. <i>C. Marschallii</i>	P
10. <i>C. latialis</i>	P ?	26. <i>C. juvenalis</i>	P ?
10. <i>C. turcica</i>	P ?	26. <i>C. aculeata</i>	P ?
10. <i>C. Triasii</i>	P ?	26. <i>C. amplexifolia</i>	P ?
10. <i>C. Raulini</i>	P ?	26. <i>C. aspera</i>	P
10. <i>C. macropus</i>	P ?	27. <i>C. Rueppellii</i>	P ?
10. <i>C. oporinoides</i>	P ?	27. <i>C. bellidifolia</i>	P
10. <i>C. turcomanica</i>	P ?	27. <i>C. bursifolia</i>	P
11. <i>C. oreades</i>	P ?	27. <i>C. nigricans</i>	P ?
11. <i>C. crocea</i>	P ?, A ?	27. <i>C. seneciooides</i>	P

Two or more subspecies exist

3. <i>C. pygmaea</i>	R ?	12. <i>C. nana</i>	R
4. <i>C. aurea</i>	R	15. <i>C. runcinata</i>	R
7. <i>C. albida</i>	R ?	19. <i>C. Reuteriana</i>	R
8. <i>C. hypochaeridea</i>	R ?	19. <i>C. pulchra</i>	R
8. <i>C. Newii</i>	R ?	20. <i>C. foetida</i>	R
8. <i>C. scaposa</i>	R ?	21. <i>C. multicaulis</i>	R
9. <i>C. suberostris</i>	R	22. <i>C. sancta</i>	R
10. <i>C. bupleurifolia</i>	R ?	23. <i>C. Dioscordidis</i>	R
11. <i>C. heterotricha</i>	R ?	25. <i>C. vesicaria</i>	R, E
11. <i>C. armena</i>	R ?	26. <i>C. setosa</i>	R

REPRODUCTION APOMICTIC, AT LEAST PARTLY.—MONOMORPHIC SPECIES

18. <i>C. chloroclada</i>	Ap ?
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(Table 1 is concluded on the next page)

TABLE 1—(Concluded)

POLYMORPHIC SPECIES			
With numerous forms		With both subspecies and forms	
15. <i>C. monticola</i>	A, E, Ap	15. <i>C. occidentalis</i>	A, E, Ap
15. <i>C. pleurocarpa</i>	A, E, Ap	15. <i>C. Bakeri</i>	A, E, Ap
15. <i>C. intermedia</i>	A, E, Ap	15. <i>C. riadocensis</i>	A, E, Ap
15. <i>C. barbigera</i>	A, E, Ap	15. <i>C. acuminata</i>	A, E, Ap
18. <i>C. Phoenix</i>	A ?, E ?, Ap ?	15. <i>C. atribarba</i>	A, E, Ap
18. <i>C. Bodinieri</i>	A ?, E ?, Ap ?	18. <i>C. rigescens</i>	A ?, E ?, Ap ?
18. <i>C. lignea</i>	A ?, E ?, Ap ?		

amount of morphological variation in a species may be very different from that indicated by the limited number of herbarium specimens at present available. Fertility relations among the individuals have not yet been tested in most of the species. Although fifty-five different species have been used in experiments on interspecific hybrids, most of them have not been subjected to intraspecific genetic analysis. For these reasons the classification into the first three of Camp and Gilly's categories must usually be tentative and be based on admittedly inadequate information. But it seemed worth while to attempt such classification, for the purpose of giving as complete a picture as possible of the kinds or probable kinds of species comprising this genus.

It should be emphasized that in classifying about one-half of the total species as monomorphic, both in table 1 and in the species descriptions, there is no intention on the part of the present author to imply that this classification is permanent. This monograph attempts to represent the genus as it is known at present, and the author is well aware that further collections may change the status of any of these "monomorphic" species. Similarly, the status of some of the polymorphic parageneons may be changed to that of rheogameons. But those which are now recognized as rheogameons will undoubtedly remain in that category, unless some future taxonomist can show good reasons for raising certain subspecies to the rank of species. It is certain, however, that the preparation of table 1 will have been worth while if it helps to correct the unfortunate impression given by Huxley (1943) that *Crepis* is a characteristically apomictic genus. The morphological peculiarities indicating polyploidy and apomixis are fairly reliable (cf. Part II, secs. 15 and 18), and it can be definitely stated that almost all of the species in the genus are not characterized by such peculiarities. In other words, all but a few of the species of *Crepis* are characterized by diploidy and by syngamy.

In the nine American species of section 15 which are known to be partly apomictic, evolution and differentiation have been determined by hybridization and polyploidy, as well as by apomixis. The resulting populations may be described as heteroploid, agamic complexes. Compared with homoploid populations, such complexes show great variability and taxonomic diversity, especially in regions where two or more of the original diploid forms occur. The application to such complexes of the usual criteria on which the species concept is based indicates that, in these complexes, there are no entities that are homologous with species which consist of homoploid sexual groups. Hence, a systematic treatment of this type of complex was proposed by Babcock and Stebbins (1938) in which species and subspecies are recognized chiefly on the basis of the distinctions between the diploid sexual forms. A large number of *formae apomicticae* which have no taxonomic status are described to

cover the individual biotypes perpetuated by apomictic reproduction. A few of these *formae apomicticae* are mentioned in the taxonomic treatment of section 15 in Part II of this monograph.

The classification of sexual, homoploid populations as species or subspecies primarily or crucially on the basis of the degree of intersterility or interfertility demonstrated by experimental crosses, as suggested by Clausen, Keck, and Hiesey (1939), has not been adopted in *Crepis*. In the first place, it was impracticable for obvious reasons, and, secondly, the general consensus among plant systematists is opposed to it. The present author had to face this question in deciding on the disposition of *Crepis foetida* and its two closest relatives, *C. eritreensis* and *C. Thomsonii* (Babcock, 1938). The last two are geographically isolated from the first, and they differ from it and from each other in morphological and physiological characters which are sufficient, in my opinion, to warrant their recognition as species, even though artificial hybrids between them were rather highly fertile. The recognition of *C. Thomsonii* and *C. eritreensis* as species is in agreement with the principles advocated by Huxley (1940, p. 22), as follows: "As Turrill (cf. Huxley, 1940, pp. 60-68) has emphasized, the fact that groups may or might show fertile intercrossing when artificially or in other ways secondarily brought together does not disprove their right to be styled species. It is the actual facts of nature, not its every potentiality, with which the systematist has to deal. The fact of their separate existence *qua* self-perpetuating interbreeding groups, together with *either* a reduction or absence of fertility in intercrossing, *or* a certain empirically evaluated degree of morphological or physiological characters, should be taken as the basis of decision."

In working out the classification of *Crepis* it was practically impossible to apply on an extensive scale the excellent methods of experimental taxonomy developed by Clausen, Keck, and Hiesey (1940). Hence, the four biosystematic units which they have adopted (Clausen, Keck, and Hiesey, 1945), namely, ecotype, eco-species, cenospecies, and comparium, are seldom mentioned in the present work. In the discussion of certain *Crepis* species, however, reference is made to ecotypes which are "genetically and physiologically distinct ecologic races." Furthermore, according to Clausen, Keck, and Hiesey (*loc. cit.*), "the eco-species approximates the species of moderately conservative taxonomists working along conventional lines." As for cenospecies and comparia, "species entirely unable to exchange genes with each other belong to different cenospecies"; whereas "distinct cenospecies which are still able to produce first generation hybrids with one another belong to one comparium." On this basis, in *Crepis*, the same comparium may include such widely separated species (cenospecies) as *C. paludosa* (sec. 1) and *C. lybica* (sec. 25), *C. aurea* (sec. 4) and *C. vesicaria* (sec. 25), *C. leontodontoides* (sec. 9) and *C. bursifolia* (sec. 27), or *C. pannonica* (sec. 10) and *C. aculeata* (sec. 26).

In contrast with the foregoing comparia are certain groups of species which belong in the same section but which also produce sterile hybrids (see pp. 58-59). For example, in section 20, six of the fifteen interspecific combinations produced vigorous but sterile hybrids. Five of these were crosses between various 5-paired species and the 4-paired *C. Kotschyana*. It has been shown (Sherman, 1946) that the inclusion of this 4-paired species in the same section with a number of 5-paired species, *primarily on morphological grounds*, is strongly supported by cytogenetic evidence. The meiotic behavior of the chromosomes in F_1 hybrids having *C. Kotschyana* for one parent and any other member of the same section for the other parent strongly indicates that all of these species must have been derived immediately from a common 5-paired ancestor. Therefore, they comprise a close group

and are properly classified in one section. But, on the sole basis of hybrid sterility, this one section is a comparium.

Thus, if we consider hybrid sterility alone, we are compelled to recognize, as comparia, groups of extremely close and relatively remote species within the same genus. Hence, the category "comparium" signifies nothing more definite than classification in the same genus, together, as a rule, with a type of genetic relationship which happens to make sterile hybrids possible. It is another illustration of the inadequacy of a single criterion to serve as the basis for the systematic classification of organisms. Nevertheless, the potential value of experimental genetics in working out many of the unsolved problems in this genus should not be overlooked. For example, the true status of the Caucasian forms of *C. paludosa* (see Part II, p. 235) or of the Uganda assemblage of variants included under *C. Rueppellii* (see Part II, p. 897) can probably be determined only by such methods.

Concerning the natural species recognized in the present treatment of *Crepis*, however, the author believes that they all probably conform to the two fundamental principles governing the existence and distribution of wild plants which are formulated by Clausen, Keck, and Hiesey (*loc. cit.*), as follows:

- 1) Natural species consist of individuals whose genes are in internal balance so that a harmonious development is assured generation after generation.
- 2) The individuals of wild species are not only balanced internally, but fit their natural environment; they are in rhythm with the seasons and adapted to the over-all conditions of temperature, moisture, wind, soil and light, as well as to the biotic elements of their environment.

At the same time it is frankly admitted that the twenty species of *Crepis*, each of which is known at present only from a single specimen or one small collection, have been recognized as species merely because their morphological distinctness and peculiarities make them unclassifiable under any other species. It remains for the future to discover whether they actually represent populations which conform to the two principles quoted above, and to the six basic criteria defined on page 34.

New species.—It has been found to be necessary or desirable to describe a total of thirty-three new species, fifteen of which are first published in this monograph. Of the total number, eight are based on a single specimen. In the opinion of the present author it is desirable to place these on record, because of the strong likelihood that each specimen actually represents at least one natural population. Some of them, like *C. Schachtii*, *C. Guioliana*, and *C. Balliana*, are of special interest because of their phyletic relations.

SUBGENERIC CATEGORIES

In all of the earlier publications on the cytobotany of *Crepis* (especially that of Babcock and Cameron, 1934), it was assumed that the three principal subdivisions of the genus which were recognized by Bentham and Hooker (1873–1876), namely, *Catonia*, *Eucrepis*, and *Barkhausia*, could be treated as subgenera. However, it became clear later that such groups cannot be recognized as natural subdivisions of the genus. This conclusion was supported by the evidence from geographic distribution, since representatives of these groups, as defined by Bentham and Hooker, occur together throughout almost the entire range of the genus. Therefore, the present arrangement of the species in twenty-seven sections was adopted as a truly natural classification. Although the sections can be grouped roughly into three divisions, namely, primitive, intermediate, and advanced, yet an attempt to key out all the species into one or another of those three major groups would be just as futile as the earlier attempts to classify them under *Catonia*, *Eucrepis*, and *Barkhausia*.

SUBSPECIFIC CATEGORIES

Early in his taxonomic experience the present author was impressed by Dr. H. M. Hall's arguments for the recognition of subspecies as the only subspecific categories worthy of receiving Latin names to be used in taxonomy. Although fully aware of the needs for names of some sort for lesser systematic units for genetical and other purposes, Hall maintained that there was no justification for encumbering the taxonomic literature and indexes with Latin names of units lower than the subspecies (Hall, 1926). Accordingly, at the outset of my work on *Crepis* it was decided that the only subspecific category to receive Latin names would be subspecies and that entities and forms of lower rank would be given numbers in the order of their discovery. Therefore, such entities and forms are listed in the taxonomic descriptions as numbered "minor variants." Whenever these entities or variants have been given names in earlier publication, the names are cited as synonyms in parentheses following the numbers, and, when the names were in the category of species, they are also included in the synonyms listed under the species descriptions. An increasing trend in taxonomic practice in the direction advocated by Hall has been evident. The recent papers of Clausen (1941) and Camp and Gilly (1943) give adequate support to this procedure.

Ideally, a subspecies is an intraspecific population with a geographic distribution which is partly isolated from that of the rest of the species but which overlaps more or less the distribution of one or more other subspecies. It may comprise one or numerous ecotypes. A species consisting of two or more subspecies is, in the sense of Rensch (1929), a *rassenkreis*, or, as defined by Camp and Gilly (1943), a *rheogameon*, or, as named by Clausen, Keck, and Hiesey (1945), an *ecospecies*. All of the polymorphic species listed in table 1 which are followed by the letter R are known to be of this type. Those followed by R? may be of this type, but available data are not sufficient to permit definitely saying so. In these and in a few species presenting special problems, such as *C. Dioscoridis* (see Part II, p. 746), the recognition of subspecies has been deemed necessary or warranted, even though the species as a whole is not a typical *rheogameon*.

In this brief discussion of taxonomic concepts, emphasis has been given to the need for a realistic view of natural populations of organisms. At the same time, recognition has been given to the difficulties arising in an attempt to make a natural classification of such populations even within a single genus. Importance is attached to a sound basis for delimiting genera and species. The classification presented in table 1 shows the kinds of species comprising the genus *Crepis*.

CHAPTER 3

CRITERIA OF CLASSIFICATION AND PHYLOGENY

THE PRINCIPAL CRITERIA for classification of the species into sections are the data on comparative morphology, chromosome number and morphology, genetics, cytogenetics, and geographic distribution. The evidence on geographic distribution is reviewed in chapter 5. Before discussing the morphologic, cytologic, and genetic criteria, the significance in this genus of the general habit of the individual plant deserves consideration. All numbered figures cited in this chapter are in Part II.

HABIT OF THE PLANT

The 196 species of *Crepis* are all herbs, unless *C. kilimandscharica* (fig. 57) might be considered a subshrub. This forestal plant develops a woody stem or caudex up to at least 1.3 meters in height and produces the usual rosette of caudical leaves at the summit. Each year the caudex is lengthened, a new rosette of caudical leaves is produced, and later the flowering stem appears. This species, therefore, in the terminology of Raunkiaer (1937), must certainly be classed as a chamaephyte. Several other perennial species develop a short, woody caudex which persists above ground. Good examples are *C. albida* subsp. *asturica* (fig. 47), *C. suffruticosa* (fig. 60), and *C. caudicalis* (fig. 73). Others sometimes develop a relatively thick, much-branched caudex at the ground level, as in *C. oporinoides* (fig. 121) and *C. xylorrhiza* (pl. 10). All such species may be considered as chamaephytes. But most of the perennial *Crepis* species are hemicryptophytes. That is, they have a perennial caudex which persists at or just below the surface of the soil, producing one or more new flower stems each year. In a few species subterranean shoots are generated, and such species may be classed as geophytes. Examples are *C. nana* and other species in section 12, *C. occidentalis* and other members of section 15, *C. frigida* and *C. elbrusensis* of section 16.

There are 143 species which are true perennials, many of which are probably short lived, and 40 species which are strictly annual plants. The other 13 species are variable with respect to duration of life, some (*C. biennis*, *C. nicaeensis*) being characteristically biennial but occasionally flowering the first season from the seed, whereas several species in section 25, including the polymorphic *C. vesicaria*, vary from perennial to annual. That the annual type has been derived from the perennial type in this genus is beyond question. Evidence on degree of reduction of the plant and its parts and on progressive adaptation to a more and more xerophytic environment, together with the well-established facts concerning phylogenetic changes in the chromosomes, all point definitely to this conclusion (see tables 2 and 11). That this relationship resembles that found in many other natural groups is shown by Hutchinson's (1926, p. 6) generalization: "Perennials are older than biennials, and from them annuals have been derived." Hutchinson (*loc. cit.*) also states that: "In certain groups, trees and shrubs are probably more primitive than herbs," a relationship which is certainly indicated in *Crepis*.

MORPHOLOGIC CRITERIA

The parts of the plant which have been found to be most useful in classification will now be discussed, with occasional allusions to the phylogenetic significance of certain resemblances and differences.

Rhizome versus taproot.—Most of the perennial species are easily classified in one or another of two distinct groups, namely, those with a rhizome which has the

gross morphology of a stem and those with a deeply penetrating true root with a central stele. There are a few species which have been placed in the second group but which appear to be intermediate, for example, *C. leontodontoides* of section 9 and *C. Reuteriana* of section 19. Such species, however, have either a deeply penetrating root, at least in some specimens, or an underground stem. The most primitive species in the genus, as determined from other morphological characters and their chromosomes, all have a rhizome. However, one species which has been placed in the first group actually appears to demonstrate the specialization of the rhizome to function as a taproot. In *C. rhaetica* the young plants have a short vertical rhizome which gradually lengthens into a deeply penetrating one simulating a taproot. (See Part II, p. 253.) The existence of such intermediate species as *C. rhaetica* and the two mentioned above is considered to support the hypothesis that, in *Crepis*, the taproot type developed from the rhizome type, an assumption which is discussed further under phylogeny (p. 65).

Caudex.—The caudex is that part of the plant which is intermediate between the root (or the rhizome) and the flower stem. In the typical hemicyclophtophytes and in the annuals the caudex is relatively short. It bears the earlier leaves of the season's growth preceding development of the flower stem. But in many of the perennial species, especially in those of the deep-rooted type, the caudex becomes elongated in older plants. It then usually bears either leaf scars or the old bases of the leaves of previous years. In those rare herbarium specimens which were so carefully collected as to preserve a part if not all of the main root, it is sometimes possible to estimate the plant's age from the consecutive series of leaf scars. Mat-forming species, such as *C. xylorrhiza*, have a caudex with several branches. In a few species these are much elongated (see *C. frigida*, Part II, fig. 189); and in certain others the plant spreads by stolons or adventitious buds on the fibrous roots, as in *C. pygmaea* (Part II, fig. 20), *C. Bungei*, and several members of section 12.

Caudical leaves.—The caudical leaves usually form a rosette with the leaves, at least the lower ones, lying on the ground. In many species the whole rosette is flat and symmetrical, but in others the younger caudical leaves are semierect. In shape, the caudical leaves range from broadly elliptic to narrowly lanceolate or almost linear; but by far the most common shape is oblanceolate. They are generally petiolate. In outline they may be entire, dentate, lyrate-pinnatifid, runcinate, or deeply pinnatifid, with broad or narrow segments. All four species in section 1 have coarsely dentate or sublyrate caudical leaves; but in *C. kashmirica* (sec. 2) they are almost entire, and in *C. pontana*, the most primitive deep-rooted species, they are entire. In the genus *Dubyaea*, the putative ancestors of *Crepis*, both entire and lyrate caudical leaves occur in different species. It is impossible to say, therefore, that one form of caudical leaf is more primitive than another. It is worth noting, however, that the lyrate pattern is of common occurrence in this genus and that it sometimes appears, as in *C. pannonica* for example, in the earliest caudical leaves but fails to appear in the later ones. In this connection the author has observed a seedling character of considerable interest. In most of the species the earliest leaves radiate symmetrically, but in *C. sibirica* and several other primitive species they are definitely congested into two groups on opposite sides of the stem. This seedling character has also been observed in *C. pannonica* of section 10. Furthermore, it has been observed that although the form of the leaves on an individual plant may be profoundly altered by a sudden, extreme change in temperature, yet plants of different species produce the characteristic form and relative size of the leaves of each species when grown under uniform, favorable greenhouse or garden conditions. Under such conditions the caudical leaves, when used

along with other characters, provide dependable criteria for classification of cultivated specimens.

Stem.—In most species of *Crepis* the stem is erect or semierect and more or less branched, with a leaf or bract subtending each branch and with several or many flower heads. The type of branching, often being distinctive, provides a good diagnostic character (see figs. 57, 67, 80). But in certain sections the species are all characterized by having scapiform, that is, one-headed stems bearing few or no leaves (see secs. 4 and 11). In some of the advanced sections, especially section 27, there is a strong tendency for the plant to have several slender, flexuous stems. In the species with branched stems the main branches may be disposed paniculately, racemously, or dichotomously; but the general plan of the inflorescence is that of a simple or compound cyme. Thus, there are many combinations of characteristic stem and branching types which are of value in classification.

Cauline leaves.—As a general rule, in the species with branched stems, the cauline leaves are gradually reduced from the base of the stem upward, but, in this, there is one outstanding exception (see sec. 18). In the more primitive species which are characterized by having cauline leaves these leaves are relatively large (see figs. 14, 23, 94). But in the advanced species they are usually extremely reduced (see figs. 240, 258, 304). The lowest cauline leaves generally exhibit intergradation in shape between the petiolate oblanceolate caudical leaves and the sessile, lanceolate middle cauline ones. In many species the middle cauline leaves are amplexicaul, that is, they clasp the stem, and the base is often sagittate or auriculate; also, various modifications of these characters occur. The uppermost leaves are usually bractlike.

Peduncles.—The peduncles, in species of branching habit, vary greatly in length and thickness in different species. For examples illustrating the greatest extremes of difference, compare *C. geracioides* (fig. 14) with *C. aspera* (fig. 291), or *C. Dioscoridis* subsp. *tubaeformis* (fig. 247) with *C. Zacintha* (fig. 249). The difference in the general aspect of the plant caused by these variations is tremendous. Another distinctive feature of the peduncle in some species is its inflation toward the base of the flower head; this is well shown in *C. Dioscoridis tubaeformis*, whereas in many species it remains about the same diameter throughout.

Flower heads.—The flower heads are commonly described as large, medium, or small; but, it being necessary in critical determinations to depend on actual measurements and other details of the involucre, these vague terms are of little value. Reduction in size of the flower heads has gone along with reduction in size of other plant parts in association with progressive advancement and specialization in this genus. But the number of florets in the heads has not followed any such consistent trend. The average number of florets in a head, however, is a useful character in distinguishing certain sections and species. Data regarding this are provided so far as possible in the descriptions in this monograph. Another feature which sometimes serves to distinguish between species is the position of the young flower heads before anthesis. In certain species they are always bent downward, that is, they are "nodding"; this is caused by the curvature of the peduncle or of the branchlet bearing two or three heads. But in certain species, for example *C. foetida* and *C. rubra*, the individual plants of a single subspecies or strain may vary in this respect. This difference in position of the young heads in the two species mentioned was found to depend on a single gene difference.

Involucre.—Differences in the involucre are among the most useful for purposes of classification and identification, as well as for establishing phylogenetic relations. In *Crepis* the involucre consists of two distinct series of scales which are called the outer and inner bracts of the involucre. In many species some of the outer bracts

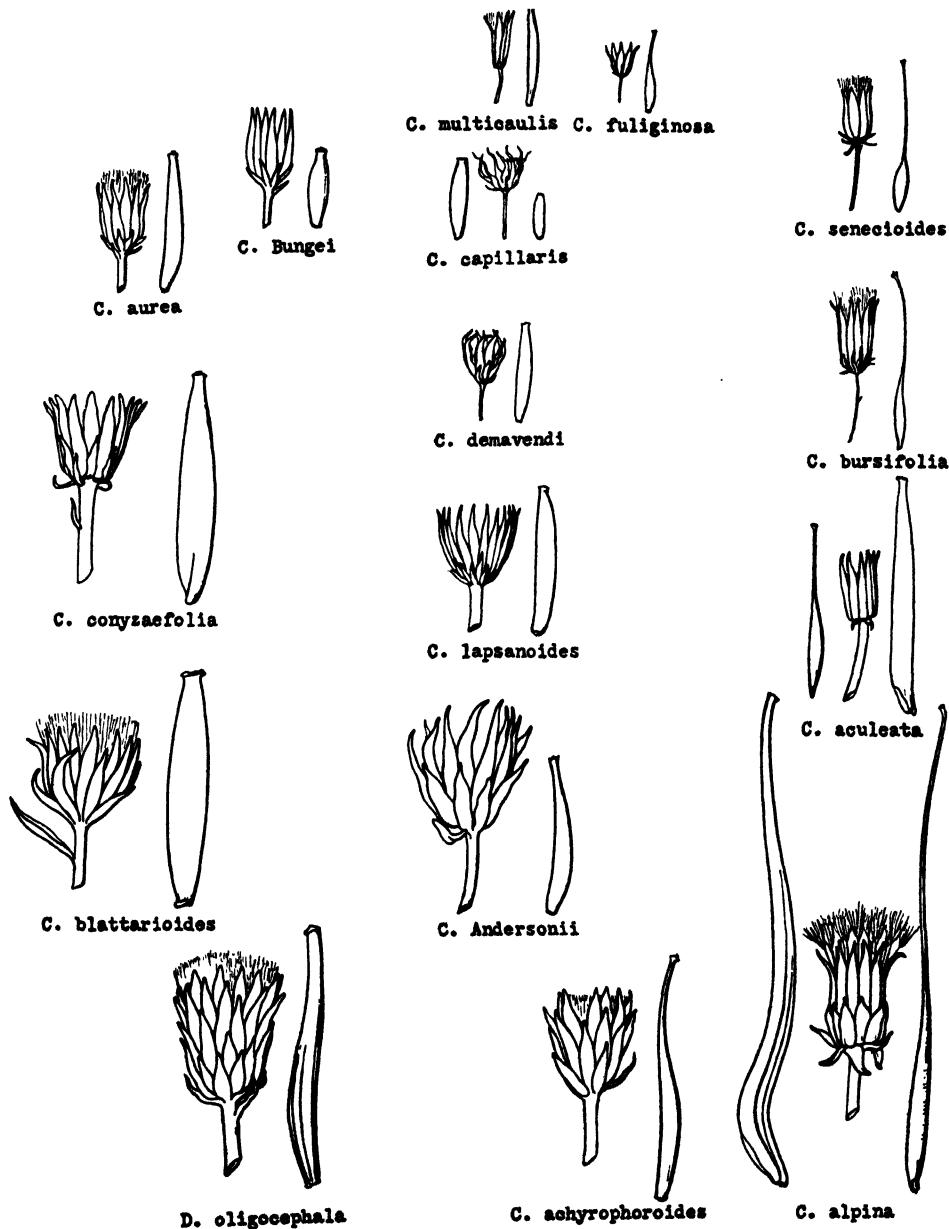


Fig. C. Fruiting heads and achenes of *Dubyaea oligocephala* and of 15 species of *Crepis* arranged in evolutionary series to show progressive reduction in size of involucre, number of bracts, and relative size of the outer bracts, as well as size of achenes, dimorphic achenes (*C. albida* and *C. aculeata*), and development of beaked achenes. (Note the extreme contrasts between the most primitive type, *D. oligocephala*, and the most advanced species, *C. fuliginosa*, *C. bursifolia*, and *C. seneciooides*.)

approach the inner ones in length, so that in an immature involucre the combined series appear as one. In addition, the outer bracts in some species are broad and overlapping or imbricate (see *C. acyphoroides* and *C. alpina*, fig. C, lower right). A fully imbricate involucre is found in that species of *Dubyaea* (*D. oligocephala*,

fig. C, lower left) which most resembles *Crepis* in several other characters. This led Schultz Bipontinus to place *D. oligocephala* with *C. albida* in Cassini's genus *Paleya*. But, in *C. albida*, when the flower head matures, the outer and inner series of bracts become clearly differentiated, as in *C. acchyrophoroides* and *C. alpina*, and in some of the subspecies of *C. albida* the two series are distinct before anthesis.

Considering the genus as a whole, it can be said that there is a general trend in *reduction* of the involucre in passing from the most primitive to the most advanced species. This reduction affects the total size of the involucre, the total number of bracts, and the relative size of the outer bracts, aspects of which are clearly illustrated in fig. C.

In addition to reduction, phylogenetic advancement in this genus is also accompanied by two distinct kinds of specialization. The most common form of specialization consists of a dorsal thickening of the inner bracts. As a result, in the mature involucre, each inner bract has a definite keel, extending from the base toward the apex, which is either narrow, making it carinate, or broad, making it navicular. This keel consists of a mass of parenchymatous cells; and such a bract is referred to as spongy-thickened. In contrast with these specialized types, the involucral bracts in the most primitive species remain essentially unchanged in fruiting heads, except that they often become indurate. The primitive type of involucre in *C. sibirica* (fig. 18, b) should be compared with the navicular type shown in *C. juvenalis* (fig. 287, g, h) and with the carinate type illustrated by *C. amplexifolia* (fig. 289, o). In many of the more advanced species the parenchymatous thickening extends into the receptacle, so that the whole lower part of the involucre becomes swollen. The keels and swollen base are usually paler in color than the rest of the involucre (see frontispiece, *C. suberostris*). The fact that in the primitive species of *Crepis* the involucre is seldom, if ever, reflexed at maturity so as to expose the ripe achenes, whereas in the advanced species the mature involucre is commonly reflexed, makes it very probable that the kind of specialization above described is actually an adaptation for more efficient seed distribution by the wind.

The other kind of specialization is much less common. In fact, it is strongly developed only in section 23. The four species in this group are more similar to one another than to any other species in the genus; yet they exhibit such remarkable diversity that a superficial view would lead to the assumption that they are not closely related. In fact, the most advanced member of the group has, until now, been considered a distinct genus (*Zacintha*). This is a weed spread widely over southern Europe, whereas the most primitive member, *C. patula* (which has also been treated as a separate genus by some taxonomists), is endemic in Algeria and Tunisia. By comparing these two species (figs. 242, l, m, and 249, g, k) their common type of involucral specialization is evident. In both species the inner involucral bracts are never reflexed, but they become much thickened and strongly indurate, so that the mature achenes are firmly enclosed. Just why this form of specialization should have proved advantageous to the species is not clear, but in *C. patula* it is associated with the possibility of distribution by running streams. One of the other two species in this section, *C. Dioscoridis* (figs. 243-247), is intermediate between the two extremes in many characters, including the involucral thickening.

Receptacle.—The receptacle, in mature involucres, provides several characters of value in classification. The surface is flat or slightly convex and is either areolate (with nearly equal small areas, each with a stipule near the center where the achene was attached), or alveolate (with the areoles separated by a ridge or fringed membrane, that is, fimbriate), or the fimbriae may be replaced by paleae. The paleae may be either bristlelike (setiform), as in sections 18 and 22, or flattened

and membranous, as in *C. foetida* subsp. *commutata*. Except for those in the two small sections and the one subspecies just mentioned, the receptacle is epaleaceous in *Crepis*. The fimbriae on alveolate receptacles, however, are often ciliate or strigose, sometimes conspicuously so.

Florets.—The complete individual floret consists of the inferior ovary, with the tubular and ligulate corolla bearing the anther tube attached by its five filaments and surrounding the style and style branches, which are pushed up through the anther tube in anthesis. The ovary is minute and superficially similar throughout the genus. Further light on the phylogenetic relations of some of the most primitive species may be obtained by a detailed study of the vascular anatomy of the ovary. In a survey of ovary anatomy in the Cichorioideae, made in connection with his monograph on *Dubyaea* and *Soroseris*, Stebbins (1940) found that a number of species of *Crepis*, including several primitive ones, have a more reduced floral anatomy than the more primitive species of *Dubyaea* (see appendix 4, pp. 169–170).

The corolla provides the following useful characters: total length, width of ligule, color of ligule, length of ligule teeth, relative length of the tube, and pubescence on the tube and base of ligule when present. The great range in length of the corolla to be found in *Crepis* is shown by comparing *C. sibirica* (fig. 13, c) with *C. multicaulis* (fig. 232, d). It may be noted here that the number of ligule teeth in *C. multicaulis* has been reduced from 5 to 4, but this has not been observed in any other species. The reduction in width of the ligule is not always proportional to the reduction in length. In certain species the ligule tends to flare out toward the summit, as shown in *C. aculeata* (fig. 288, h). In certain others it tends to fold up around the anther tube so that it is difficult to determine its width (cf. *C. foetida*, fig. 217, e). The color of the ligules in almost all of the species is some shade of yellow; but there are three pink-flowered species, *C. rubra*, *C. incana*, and *C. incarnata*; also, one white-flowered species, *C. albiflora*, and white-flowered plants of *C. rubra* occur in gardens. Many of the yellow-flowered species also have a reddish stripe on the outer face of the marginal florets, but others lack red color entirely. In *C. bursifolia* the red dorsal stripe is replaced by one of bluish-green. The length of the ligule teeth is very variable between species, though reduction with phylogenetic advancement is the general rule as to length as well as to the prominence of the glandular dorsal crest or anterior knob or lip at the apex of each tooth. In certain species this glandular mass takes on a very distinctive shape which may be helpful in identification. That the relative length of the corolla tube is also variable throughout the genus is seen by again comparing *C. sibirica* with *C. multicaulis* or with *C. achyrophoroides* (fig. 52, d) in both of which the tube is nearly half as long as the whole corolla. But in most of the species the tube is about one-third the length of the corolla. When pubescence is present on the corolla tube it may consist of any one of several types of trichomes or a mixture of two or three kinds. One of the most unusual combinations in *Crepis* is that of *C. achyrophoroides* (fig. 52, d), in which there is a cluster of long, many-celled, acicular trichomes just at the summit of the tube, which is also densely covered with very short, pointed trichomes. The cluster of trichomes at the summit of the tube is frequently present in certain other genera of the Crepidinae, such as *Lactuca*, but is very rare in *Crepis*.

The anther tube and filaments also present a great variety of relative sizes, as is shown by comparing *C. sibirica* (fig. 13, d) with *C. multicaulis* (fig. 232, e) and *C. Zocintha* (fig. 249, m). Similarly with the anther appendages, which are generally longer and broader in the primitive species versus shorter and narrower in the advanced ones; and, as between species, there is considerable variation in their shape.

The style branches also vary widely in length and considerably in width (cf. *C. sibirica* and *C. multicaulis*). But throughout the genus they are semicylindric in shape and are generally attenuate toward the apex. In color the style branches may be dark green, bright yellow, or some intermediate shade.

Achenes.—In this genus the achenes present a remarkable diversity in color, size, and shape, in the details of their apical and basal parts, and in the ribs. But within a species or a subspecies there is relative constancy with respect to all these features. It is for this reason that the identification of the fossil achenes which are illustrated in plate 1 is made with confidence respecting its correctness. In all 3 of these species the achenes are monomorphic, which is true of all the species in sections 1 to 18. In all of these 135 species the achenes are essentially monomorphic, making due allowance, of course, for some differences in shape between the marginal and innermost achenes in a head, since such differences are usually continuous in passing from the marginal ones toward the center of the receptacle. It is only in the advanced sections, 19, 20, 22, 23, 25, and 26, that some or all of the species have dimorphic achenes. Dimorphism in the achenes, therefore, accompanies phylogenetic advancement in this genus. It may well be a form of specialization which somehow aids in the perpetuation of the species. The beak or slender stipe, bearing the pappus at its apex, is another specialized feature of the achenes in many species, since it undoubtedly aids in the distribution of the fruits by the wind. None of the 26 most primitive species (secs. 1-6) has beaked achenes (see fig. C), whereas in all but one of the 27 most advanced species (secs. 25-27) the achenes are beaked, and in the most advanced species of all the beak is extremely fine and delicate (see fig. C). In section 20, also, all of the species have long-beaked achenes, but these species are somewhat more primitive in other characters than those of the most advanced sections (fig. C, lower right). In the rest of the sections most of the species have beakless achenes, but in sections 7, 12, 19, and 24 the most advanced species have developed beaks. In many of the older treatises on *Crepis* the presence or absence of a beak on the achenes was the chief or sole diagnostic character used in classifying under *Barkhausia* or *Crepis*. Since some of the species in such a primitive group as section 8 have more or less definitely beaked achenes, and since one or more such species occur in several intermediate sections, this character obviously cannot be used for such a purpose.

Pappus.—The pappus setae, although simple, barbellulate bristles, also present some useful diagnostic characters. The color ranges from pure white, as in most species, through dusky shades to yellow. The length varies from less than one millimeter in *C. patula* to about one centimeter in some of the most primitive species. The number of series of setae borne on the pappus disk varies from 4 or 5 down to 1. And the thickness of the setae, as indicated by their width at the base, varies from about 20 to about 80 microns. This results in marked differences in degree of rigidity or brittleness as opposed to softness or plianceness. It was found by Stebbins (1940) that most *Crepis* species have less coarse pappus setae than are found in *Dubyaea*. But the pappus setae of some of the primitive species of *Crepis* resemble those of *D. chilensis*, as illustrated by Stebbins (*op. cit.*, fig. 1, a, b).

Indumentum.—The indumentum of the vegetative parts and involucre may consist of any one of three general types: (1) tomentum of various shades from white to brown and various degrees of thickness; (2) glandless hairs or setae of various lengths and colors from transparent to black; and (3) gland-bearing hairs of similar diversity in size and color. The presence of a certain type or combination of types of indumentum is often fairly constant within a species or subspecies and serves as a valuable additional criterion of classification.

CYTOLOGIC CRITERIA

The chromosomes of related genera.—The earlier reports on chromosome numbers in genera close to *Crepis* have been supplemented by Babcock, Stebbins, and Jenkins (1937), who reported on two species of *Dubyaca*, nine of *Prenanthes*, twenty-five of *Lactuca*, two of *Youngia*, two of *Ixeris*, and one of *Cephalorrhyncus*. These data, added to those reported by others, led to several conclusions, among which the following are pertinent here:

- 1) The somatic chromosome numbers 16 and 32 occur in *Prenanthes* subg. *Nabalus*; 18 in subg. *Euprenanthes*; 16 in the genus *Dubyaea*; 16, 18, 34, and 36 in the various subgenera of *Lactuca*; 18 in *Cephalorrhyncus*; and 16 or 32 in all the species of *Youngia* thus far reported, except *Y. tenuifolia*, which is a polyploid complex with 15, 20, and 24 chromosomes.
- 2) The more primitive diploid number in *Dubyaca*, *Prenanthes*, and *Youngia* is probably 16. In *Lactuca* more of the primitive species have this number, and more of the advanced species have 18, but both numbers may have existed since the formation of the genus.
- 3) The primitive somatic numbers for the *Crepidinae* are probably 16 and 18, whereas 12, 10, 8, and 6 were derived from them by some process of reduction.
- 4) The hypothesis that reduction in absolute size of the chromosomes often accompanies evolutionary advancement is borne out by the study of these genera, although certain exceptions were found.
- 5) The hypothesis that in primitive species most of the chromosomes have median constrictions and the chromosomes of a haploid set are nearly equal in size is borne out by this study, as is the hypothesis that, with advancing evolution, subterminal constrictions are evolved and the chromosomes of a set become unequal in size. It is suggested that the early differentiation of genera in the *Crepidinae* was accompanied by less structural differentiation of the chromosomes than was the evolution of species groups among the more highly evolved and diversified subgenera.

Thus, the available evidence from closely related genera certainly indicates that similar relations exist between karyotype evolution and phylogenetic advancement to those which exist in *Crepis*. In order to fill the gap between *Crepis* and *Dubyaea*, it is necessary to assume that ancestral species of either genus with 14 somatic chromosomes must have existed but may now be extinct. It is evident, however, that much further botanical exploration in Asia, accompanied by study of the chromosomes, is needed.

The chromosomes of Crepis.—The evidence from *Crepis* on chromosomes and classification and on chromosomes and phylogeny has been reviewed in chapters 1 and 4. In table 2 are listed the 113 species of *Crepis* which have been studied cytologically. They are arranged in approximate phylogenetic sequence, with the section number given in the left-hand column. To the right of each species the somatic chromosome number is given, together with the "chromosome class," that is, whether the species is diploid, dysploid, tetraploid, octoploid, allopolyploid, or euploid. Also, the classification of each species in accordance with the method of reproduction and duration of life is given. A brief examination of this table is sufficient to make clear the general parallelism which exists between phylogenetic advancement, as determined in arranging the sections on a morphological basis, and reduction in chromosome number. The diploid and polyploid species are characterized by sexual reproduction, with the outstanding exception of 9 of the American species in section 15. It should be noted also that the 5 species in section 18 are probably apomictic, but none of them has thus far been studied in living condition.

TABLE 2

CLASSIFICATION OF 113 SPECIES OF *CREPIS* IN ACCORDANCE WITH SECTION, SOMATIC CHROMOSOME NUMBER, CHROMOSOME CLASS, METHOD OF REPRODUCTION, AND DURATION OF LIFE

Section	Species	Somatic chromosomes		Reproduction	Duration
		Number	Class*		
1	<i>C. sibirica</i> ...	10	D	sexual	perennial
1	<i>C. geracioides</i> ...	12	D	sexual	perennial
1	<i>C. viscidula</i> ...	12	D	sexual	perennial
1	<i>C. paludosa</i> ...	12	D	sexual	perennial
2	<i>C. kashmirica</i> ...	12	D	sexual	perennial
3	<i>C. pygmaea</i> ...	12	D	sexual	perennial
4	<i>C. terglouensis</i> ...	12	D	sexual	perennial
4	<i>C. Jacquinii</i> ...	12	D	sexual	perennial
4	<i>C. aurea</i> ...	10	D	sexual	perennial
4	<i>C. hokkaidoensis</i> ...	8	D	sexual	perennial
4	<i>C. chrysantha</i> ...	8	D	sexual	perennial
4	<i>C. polytricha</i> ...	16	T	sexual	perennial
4	<i>C. albiflora</i> ...	8	D	sexual	perennial
5	<i>C. lapsanoides</i> ...	12	D	sexual	perennial
5	<i>C. lyrata</i> ...	12	D	sexual	perennial
5	<i>C. mollis</i> ...	12	D	sexual	perennial
5	<i>C. willemetoides</i> ...	12	D	sexual	perennial
5	<i>C. hierosolymitana</i> ...	12	D	sexual	perennial
5	<i>C. montana</i> ...	12	D	sexual	perennial
5	<i>C. Mungierii</i> ...	12	D	sexual	perennial
6	<i>C. pontana</i> ...	10	D	sexual	perennial
6	<i>C. conyzaeifolia</i> ...	8	D	sexual	perennial
6	<i>C. blattarioides</i> ...	8	D	sexual	perennial
7	<i>C. albida</i> ...	10	D	sexual	perennial
8	<i>C. kilimandscharica</i> ...	8	D	sexual	perennial
8	<i>C. alpestris</i> ...	8	D	sexual	perennial
8	<i>C. suffruticosa</i> ...	8	D	sexual	perennial
8	<i>C. hypochaeridea</i> ...	8	D	sexual	perennial
8	<i>C. Newii</i> ...	8	D	sexual	perennial
8	<i>C. scaposa</i> ...	8	D	sexual	perennial
9	<i>C. tingitana</i> ...	10	D	sexual	perennial
9	<i>C. leontodontoides</i> ...	10	D	sexual	perennial
9	<i>C. suberostris</i> ...	10	D	sexual	perennial
10	<i>C. ciliata</i> ...	± 40	O	sexual	biennial
10	<i>C. biennis</i> ...	± 40	O, A?	sexual	biennial
10	<i>C. pannonica</i> ...	8	D	sexual	perennial
10	<i>C. latialis</i> ...	8	D	sexual	perennial
10	<i>C. chondrilloides</i> ...	8	D	sexual	perennial
10	<i>C. Baldaccii</i> ...	10	D	sexual	perennial
10	<i>C. Triasii</i> ...	8	D	sexual	perennial
10	<i>C. Raulini</i> ...	10	D	sexual	perennial
10	<i>C. oporinoides</i> ...	8	D	sexual	perennial
10	<i>C. incana</i> ...	16	T	sexual	perennial
10	<i>C. taygetica</i> ...	± 40	O?	sexual	perennial
11	<i>C. Schachtii</i> ...	10	D	sexual	perennial
11	<i>C. bituminosa</i> ...	10	D	sexual	perennial
11	<i>C. oreades</i> ...	8	D	sexual	perennial
11	<i>C. crocea</i> ...	16	T, A?	sexual	perennial
11	<i>C. Hookeriana</i> ...	8	D	sexual	perennial
11	<i>C. Robertioides</i> ...	8	D	sexual	perennial
12	<i>C. flexuosa</i> ...	14	D	sexual	perennial
12	<i>C. nana</i> ...	14	D	sexual	perennial
12	<i>C. elegans</i> ...	14	D	sexual	perennial
13	<i>C. gymnopus</i> ...	8	D	sexual	perennial
13	<i>C. praemorsa</i> ...	8	D	sexual	perennial
13	<i>C. incarnata</i> ...	8	D	sexual	perennial
14	<i>C. Bungei</i> ...	8	D	sexual	perennial

* Abbreviations in this column stand for the terms indicated: D, diploid; Dy, dysploid; T, tetraploid; O, octoploid; A, allopolyploid; E, euploid. For definitions of these terms, see p. 38.

TABLE 2—(Continued)

Section	Species	Somatic chromosomes		Reproduction	Duration
		Number	Class*		
14	<i>C. tectorum</i> ...	8	D	sexual	annual
15	<i>C. monticola</i> ...	22-88	A, E	apomictic	perennial
15	<i>C. occidentalis</i> ...	22-88	A, E	apomictic	perennial
15	<i>C. Bakeri</i> ...	22-55	A, E	apomictic	perennial
15	<i>C. modocensis</i> ...	22-88	A, E	apomictic	perennial
15	<i>C. pleurocarpa</i> ...	22-88	A, E	apomictic	perennial
15	<i>C. acuminata</i> ...	22-88	A, E	apomictic	perennial
15	<i>C. atribarba</i> ...	22-88	A, E	apomictic	perennial
15	<i>C. intermedia</i> ...	33-88	A, E	apomictic	perennial
15	<i>C. barbigera</i> ...	44-88	A, E	apomictic	perennial
15	<i>C. runcinata</i> ...	22	A	sexual	perennial
19	<i>C. Reuteriana</i> ...	8	D	sexual	perennial
19	<i>C. palaestina</i> ...	8	D	sexual	annual
19	<i>C. pulchra</i> ...	8	D	sexual	annual
19	<i>C. Stojanovi</i> ...	8	D	sexual	annual
19	<i>C. pterothecoides</i> ...	8	D	sexual	annual
20	<i>C. alpina</i> ...	10	D	sexual	annual
20	<i>C. syriaca</i> ...	10-18	Dy	sexual	annual
20	<i>C. rubra</i> ...	10	D	sexual	annual
20	<i>C. foetida</i> ...	10	D	sexual	annual
20	<i>C. eritreensis</i> ...	10	D	sexual	annual
20	<i>C. Thomsonii</i> ...	10	D	sexual	annual
20	<i>C. Kotschyana</i> ...	8	D	sexual	annual
21	<i>C. multicaulis</i> ...	10	D	sexual	perennial
22	<i>C. sancta</i> ...	10	D	sexual	annual
23	<i>C. patula</i> ...	8	D	sexual	perennial
23	<i>C. Dioscoridis</i> ...	8	D	sexual	annual
23	<i>C. multiflora</i> ...	8	D	sexual	annual
23	<i>C. Zacintha</i> ...	6	D	sexual	annual
24	<i>C. nicaeensis</i> ...	8	D	sexual	biennial
24	<i>C. capillaris</i> ...	6	D	sexual	annual
24	<i>C. parviflora</i> ...	8	D	sexual	annual
24	<i>C. neglecta</i> ...	8	D	sexual	annual
24	<i>C. corymbosa</i> ...	8	D	sexual	annual
24	<i>C. fuliginosa</i> ...	6	D	sexual	annual
24	<i>C. cretica</i> ...	8	D	sexual	annual
24	<i>C. apula</i> ...	8	D	sexual	annual
24	<i>C. Suffreniana</i> ...	8	D	sexual	annual
25	<i>C. Clausonis</i> ...	8	D	sexual	perennial
25	<i>C. Fontiana</i> ...	8	D	sexual	perennial
25	<i>C. Bourgeau</i> ...	8	D	sexual	perennial
25	<i>C. canariensis</i> ...	8	D	sexual	perennial
25	<i>C. divaricata</i> ...	8	D	sexual	per. or bi.
25	<i>C. Noronhaea</i> ...	8	D	sexual	per. or bi.
25	<i>C. libyca</i> ...	8	D	sexual	per. or bi.
25	<i>C. vesicaria</i> ...	8-16	D, E, A?	sexual	per., bi., an.
25	<i>C. Marschallii</i> ...	8	D	sexual	biennial
26	<i>C. juvenalis</i> ...	8	D	sexual	annual
26	<i>C. aculeata</i> ...	8	D	sexual	annual
26	<i>C. amplexifolia</i> ...	8	D	sexual	annual
26	<i>C. aspera</i> ...	8	D	sexual	annual
26	<i>C. setosa</i> ...	8	D	sexual	annual
27	<i>C. bellidifolia</i> ...	8	D	sexual	perennial
27	<i>C. bursifolia</i> ...	8	D	sexual	perennial
27	<i>C. nigricans</i> ...	8	D	sexual	annual
27	<i>C. senecioides</i> ...	8	D	sexual	annual

* Abbreviations in this column stand for the terms indicated: D, diploid; Dy, dysploid; T, tetraploid; O, octoploid; A, allopolyploid; E, euploid. For definitions of these terms, see p. 35.

GENETIC CRITERIA

Crossability, vigor, and fertility.—The original data on the interspecific hybrids made between 1920 and 1939 are summarized in the list of interspecific combinations at the end of this chapter. These include reports on 195 combinations in which 55 different species were involved. The combinations are arranged in five subdivisions, as follows: *A*. Diploid species in the same section (intrasectional). *B*. Diploid species in different sections (intersectional). *C*. One species polyploid—both in the

TABLE 3
INTERSPECIFIC HYBRIDIZATION IN CREPIS—SUMMARY OF DIPLOID SPECIES

Groups and sections represented in the combinations	Total combinations attempted	Number of combinations giving no hybrids	Number of combinations giving one or more hybrids	Hybrids vigorous: medium to high fertility	Hybrids vigorous: low fertility or sterile	Hybrids weak: low fertility or sterile
Intrasectional combinations*						
I. Secs. 6 and 9.....	4	1	3	..	1	2
II. Secs. 10, 19, 20.....	21	1	20	5	12	3
III. Secs. 24, 25, 26.....	18	1	17	6	9	2
Totals.....	43	3	40	11	22	7
Intersectional combinations*						
I. (1, 4, 5, 6, 7, 8, 9).....	8	4	4	..	3	1
II. (10, 13, 14, 19, 20).....	9	7	2	2
III. (23, 24, 25, 26, 27).....	34	6	28	..	22	6
I × II.....	17	10	7	..	2	5
II × III.....	35	14	21	..	11	10
I × III.....	24	9	15	..	9	6
Totals.....	127	50	77	..	47	30

* This grouping of the sections into I, more primitive; II, intermediate; III, more advanced, was used instead of the grouping according to type of root (see chapter 4, table 4) because there were no intrasectional hybrids in sections 1-4, 13, and 21. The totals of intrasectional and intersectional combinations and hybrids are the same with either system of grouping.

same section. *D*. One species polyploid—the two in different sections. *E*. Both species polyploid. In each part the hybrid combinations are arranged by sections and, under each section, in ascending order from more primitive to more advanced species; thus, this facilitates the consultation of data pertaining to any particular section or combination of sections. Concerning hybrid fertility, the original data were, for the most part, expressed in percentages estimated from the proportion of plump achenes produced by the hybrids, usually under open-pollination. But in some instances the degree of fertility was originally recorded as very low, low, medium, or high. When recorded as actual percentages, these were expressed in intervals of 5, except in those of very low fertility, which were recorded as 1, 2, 3, 4, or 5 per cent. For the sake of uniformity the actual percentages found in the original data have been classified as follows: very low, 1-5 per cent; low, 10-25 per cent; medium, 30-65 per cent; high 70-100 per cent.

Parts *A* and *B* have the most significance with reference to interspecific relationships, partly because these data are more numerous, and especially because the expression of hybrid fertility is not complicated by polyploidy. These data are

summarized in table 3. In this representation two features are most striking. Whereas 93 per cent of the intrasectional combinations produced hybrids, and 27.5 per cent of these hybrids were vigorous with medium to high fertility, only 60 per cent of the intersectional combinations produced hybrids, not one of which was both vigorous and of medium or high fertility. Although crossability alone is of dubious value as an index of relationship, yet the difference between these intra- and intersectional crosses is so striking that some degree of significance must be inferred. Moreover, this is strongly supported by the differences in hybrid vigor, as well as in fertility. Only seven, i.e., 17.5 per cent of the forty intrasectional hybrids, as compared with thirty, i.e., 40 per cent of the seventy-seven intersectional hybrids were described as weak and of low fertility or sterile; whereas thirty-three or 82.5 per cent of the intrasectional hybrids were vigorous, and one-third of these were medium or highly fertile, but only forty-seven or 60 per cent of the intersectional hybrids were vigorous, and all were of low fertility or sterile. This evidence certainly indicates that the sections represented by these interspecific hybrids are groups of species which are more closely related to one another than to the members of other sections. To this extent it supports the sectional scheme of classification here adopted.

The data on intersectional crosses in which one parent is polyplloid are sufficiently numerous to warrant comparison with the foregoing. Of the twenty combinations attempted, twelve failed to produce hybrids, seven produced one or more vigorous hybrids of low fertility or sterile, and one produced a weak sterile hybrid. These data are in general agreement with the data on diploid intersectional hybrids.

Comparative genetics.—Less work on the comparative genetics of *Crepis* species has been done than was intended at the outset of these investigations. This was due to the early discovery of the possibilities of interspecific hybridization and the long period of time required for assembling the wild species in living condition and for cytologically studying the species and certain hybrids. As a result of the research of several co-workers and students, however, it is possible to present some evidence, based on segregation in hybrid populations, which indicates at least the existence of genic homology between different species.

Plant stature.—Among the twenty-two characters in *Crepis capillaris* which were studied by Collins (1924) were two or more dwarf types which behaved as Mendelian recessives when crossed with plants of normal stature. In *Crepis tectorum* there are two wild dwarf forms in Scandinavia, one of which (fa. *pygmaea* Sjöstr.) is also recessive to tall stature and is inherited according to Mendelian principles.

Leaf "shape," pinnatifid versus dentate margin.—In *C. capillaris*, Collins (*loc. cit.*) reported that pinnate margin is dominant to dentate margin and due to a single gene difference. In a cross between two subspecies of *C. foetida*, Babcock and Cave (1938) found the same relation between pinnatifid and dentate leaves.

Anthocyanin.—The general occurrence of anthocyanin in *Crepis* species was pointed out by Collins (*Science*, 63: 52, 1928), who had found large and small amounts of the pigment in the leaves of *C. capillaris* to be inherited as Mendelian characters. He also reported a pure green plant of *C. Dioscoridis* which gave a 3:1 ratio in F_2 when crossed with a normally pigmented plant. It was reported by Babcock and Navashin (1930) that in *C. neglecta* the presence and absence of anthocyanin in the leaves behave as a monohybrid difference. They also reported (*loc. cit.*) that the white-flowered horticultural variety of *C. rubra* behaves as a simple recessive when crossed with typical pink-flowered forms. Babcock and Cave (1938) found anthocyanin leaf spots to be present in some strains of *C. foetida*.

and absent in others, whereas it was always absent in *C. eritreensis* and always present in *C. Thomsonii*. In crosses between the last species and *C. eritreensis* and between *C. Thomsonii* and certain strains of *C. foetida* lacking these leaf spots, the inheritance was, for the most part, typical of a monohybrid. The same authors (*loc. cit.*) reported that *C. Thomsonii* and *C. eritreensis* have red ligule teeth on all the florets, whereas in *C. foetida* all except the outer row of florets have yellow teeth. In ten crosses between one or the other of the first two species and seven strains of *C. foetida*, all the F_1 plants had red ligule teeth, and in six F_2 families there was close approximation to the 3:1 ratio; but the other four F_2 families showed extreme deviations from the monohybrid ratio. The following evidence on a similar character in species of section 25 suggests a plausible explanation for these deviations. Jenkins (1939), working with four closely related species of section 25, found that *C. Noronhaea* has a conspicuous red stripe on the dorsal surface of the outer row of ligules and that *C. divaricata* and *C. canariensis* lack this feature; he also noted that it was present in *C. vesicaria taraxacifolia* but absent in *C. vesicaria andryaloides*. In all the crosses in which one parent had the stripe and the other had none and when both parents were homozygous, a ratio of 3:1 (three striped and one nonstriped) occurred in F_2 . Some of the F_1 hybrids from these species crosses, however, failed to show the stripe, even though their progeny segregated as stated above. Jenkins inferred that this was because these F_1 hybrids did not have the proper genic milieu for the development of the stripe; that is, he held that the presence of this character requires not only the dominant gene but also a definite genic background for its expression.

Chlorophyll reduction.—In *C. capillaris*, Collins (1924) discovered at least three different recessive genes for reduction of the chlorophyll; and a recessive gene causing chlorophyll reduction was reported by Babcock and Navashin (1930) in *C. Dioscordis*.

Erect versus nodding flower buds.—In most species of *Crepis* the heads are erect in all stages of development; but in certain species, viz., *C. neglecta* (sec. 24) and its closest relatives, the branchlets or peduncles bearing young heads are strongly bent downward. This character appears also in the distantly related *C. carbonaria* (sec. 7); and in section 20, seven of the nine species have the young heads always nodding, whereas in *C. alpina* they are always erect; and in *C. foetida* some forms have them nodding and some erect. In crosses between *C. rubra*, with nodding buds, and a form of *C. foetida*, with erect buds, Poole (1932) reported monohybrid inheritance. Similar results were reported by Babcock and Cave (1938) from crosses between *C. eritreensis* or *C. Thomsonii*, both with nodding buds, and a form of *C. foetida*, with erect buds.

Paleae.—A unique plant of *C. capillaris*, in which every floret was subtended by a bractlike palea, was discovered by Collins (1921, 1924) who reported that it was conditioned by a single recessive gene. In *C. foetida commutata* similar paleae are present on the receptacle, and they have been found in a few forms of *C. foetida rhoeadifolia*; but the latter subspecies usually lacks true paleae, and they have never been found in other forms of *C. foetida*, nor in its close relatives, *C. eritreensis* and *C. Thomsonii*. Babcock and Cave (1938) reported that from ten crosses involving *C. foetida commutata* as one parent and either *C. Thomsonii*, *C. eritreensis*, or a form of *C. foetida* lacking paleae as the other parent, all the F_1 plants had paleae, but only one F_2 family gave a 3:1 ratio, whereas six F_2 families gave ratios approximating 15:1 and three produced a trihybrid hybrid ratio close to 51:13. These results show that presence and absence of paleae in *C. foetida* and its two nearest relatives depend on at least three pairs of genes. In this connection it is

significant that in *C. sancta*, which has setuliferous paleae on the receptacle, wild forms with the receptacle naked have been discovered (see Part II, p. 733, m.v. 1).

Self-incompatibility.—Some species of *Crepis*, like *C. tectorum*, *C. pulchra*, *C. scaposa*, *C. multicaulis*, and *C. alpina*, are highly if not completely self-compatible. At least they usually produce selfed seed abundantly under favorable environmental conditions. Some species, like *C. capillaris*, are self-compatible but variable in the quantity of selfed seed produced. Many species, however, produce only small quantities of selfed seed, even under favorable conditions; and some are definitely known to be characterized by self-incompatibility, even though, like other self-incompatible plants, they occasionally produce a few selfed seeds. This is true in *C. foetida rhoeadifolia* and *C. foetida commutata*; but in *C. foetida vulgaris* and in *C. Thomsonii* and *C. eritreensis* the plants are self-compatible. From preliminary experiments Babcock and Cave (1938) obtained data indicating that *C. Thomsonii* and *C. eritreensis* differ more from *C. foetida* in the genetic nature of their self-compatibility than the several forms of *C. foetida*, which were used, differ among themselves. Their results also indicated that the genetic basis of self-incompatibility in *C. foetida* was different from any genetic scheme for incompatibility that had previously been reported. M. B. Hughes (1943) made a thorough study of self-incompatibility in *C. foetida rhoeadifolia* from which he concluded that, although a single series of alleles is responsible for the phenomenon, yet, in order to explain aberrant results from reciprocal crosses between two of his seven genotypically different groups, it is necessary to assume that one member of the series of alleles can be either strongly or weakly potent. It is not unlikely that other modifications of the usual genetic scheme for self-incompatibility occur among the many "self-sterile" species of *Crepis*.

Size differences.—Although certain differences in size, such as plant stature, are determined by only one or two genes, almost all of the quantitative differences between those closely related species which have been studied genetically are conditioned by several or many genes, each having a relatively small effect. For example, in hybrids between *C. divaricata* ($n = 4$) and *C. vesicaria taraxacifolia* ($n = 4$), Jenkins (1939) obtained data on the inheritance of leaf length, length-width ratio in the leaves, diameter of the open flower heads, height of stem, ratio of height to spread of plant, achene length, and length of the beak of the achene. The F_1 hybrids were intermediate and the F_2 exhibited blending inheritance with a range similar to that of the parental extremes. But for most of these characters no recovery of types corresponding to the parents was found, which indicates that the intermediate combinations were mostly able to survive and that a great many genic differences exist between the two species. Furthermore, no new characters appeared in either F_1 or F_2 , which indicates that the gene systems in the two species were essentially the same. Similar generalizations could be made regarding hybrids between all four of the closely related species with which he worked (see p. 17). Babcock and Cave (1938) presented some evidence of multiple factors conditioning quantitative differences in *C. foetida*, *C. eritreensis*, and *C. Thomsonii*, all with $n = 5$. In both of these groups of closely related species the F_1 hybrids were perfectly regular in diakinesis and meiotic metaphase, which indicates that the structure of the chromosomes is closely similar in the several species in each of the two groups. Thus, the genes of one species can be transferred to another species and, since meiosis is regular and the fertility of the hybrids is sufficient to produce numerous progeny, either ordinary Mendelian or multiple gene inheritance ensues according to the nature of the differences observed. From this it may be inferred that the only genetic process of importance in the differentiation within these two groups of

species is gene mutation. In certain others, however, it is clear that other genetic processes have been partly responsible for speciation (see the following section).

Cytogenetics of interspecific hybrids.—The literature in this field up to 1941 has been reviewed (cf. Babcock, 1942), and it is only necessary here to point out certain generalizations and conclusions which have a direct bearing upon interspecific relations in the genus.

Hybrids with high meiotic regularity.—The genetic relations between diploid species, with the same chromosome numbers and nearly identical karyotypes, have been studied in two groups of closely related species, one in section 20 (Babcock and Cave, 1938), the other in section 25 (Jenkins, 1939). In the F_1 hybrids meiosis is just as regular as in the parent species, which indicates that the chromosomes of these species contain no considerable structural differences. In the F_2 generation certain qualitative characters exhibit simple Mendelian ratios, but most of the quantitative differences behave as though conditioned by numerous genes. Hence, it appears that such species differ mainly with respect to their genes and that the decreased fertility which is characteristic of their hybrids is due to such genic differences. This has an important bearing on the causes of evolution in the genus (see p. 24).

Reduced metaphase pairing and interspecific relationship.—The earlier evidence on irregularities in chromosome distribution in the first meiotic division in interspecific hybrids was reviewed by Babcock and Emsweller (1936). Thirteen different hybrid combinations were studied, five by Avery (1930), two by Hollingshead (1930b), three by Babcock and Clausen (1929), one by Müntzing (1934), and two by Emsweller (Babcock and Emsweller, 1936). But three of these hybrids, one by Avery and two by Hollingshead, had as one parent *C. capillaris*, which was found to be highly variable itself in amount of metaphase pairing. For the sake of brevity and simplicity, these data are omitted here. The ten hybrids under consideration are listed below, in ascending order with respect to the degree of primitiveness of the sections represented in the parents.

SECTIONS	SPECIES AND HAPLOID NUMBERS	MEAN NUMBERS OF BIVALENTS
4-9.	<i>aurea</i> 5 \times <i>leontodontoides</i> 5	4.7 \pm .16
9-14.	<i>leontodontoides</i> 5 \times <i>tectorum</i> 4	2.0 \pm .26
9-24.	<i>leontodontoides</i> 5 \times <i>parviflora</i> 4	2.5 \pm .47
9-25.	<i>leontodontoides</i> 5 \times <i>Marschallii</i> 4	1.6 \pm .22
14-25.	<i>tectorum</i> 4 \times <i>vesicaria</i> <i>taraxacifolia</i> 4	2.8 \pm .27
23-25.	<i>Dioscoridis</i> 4 \times <i>divaricata</i> 4	1.8 \pm .23
24-26.	<i>nicaeensis</i> 4 \times <i>setosa typica</i> 4	3.9 \pm .21
24-26.	<i>nicaeensis</i> 4 \times <i>setosa</i> <i>Topaliana</i> 4	3.4 \pm .18
26-26.	<i>aculeata</i> 4 \times <i>aspera</i> 4	3.5 \pm .18
26-27.	<i>aspera</i> 4 \times <i>bursifolia</i> 4	2.5 \pm .28

It is a generally accepted theory that the pairing of the chromosomes in the meiotic prophases depends upon genic homology. The mean number of bivalents counted at first meiotic metaphase in these hybrids ranges from $1.6 \pm .22$ to $4.7 \pm .16$, and it will be noted that the standard errors are relatively small. This certainly indicates marked differences in the degree of genic homology between the species used in the various crosses.

The first four hybrid combinations, which involve *C. leontodontoides* of section 9, make an instructive series in themselves. The high meiotic regularity found in the hybrids between *C. aurea* and *C. leontodontoides* strongly supports the evidence from comparative morphology, which indicates that *C. leontodontoides* is actually close to the more primitive species, *C. tingitana*, also of section 9. On the other hand, the hybrids between *C. leontodontoides* and three advanced species showed reduced

regularity, forming only about half the number of metaphase pairs that would be possible in a hybrid between a 5-paired and a 4-paired species. It is worth noting also that *C. aurea* and *C. leontodontoides* are indigenous in the same geographic area, although the former is montane and the latter is found in low altitudes. But *C. tectorum*, *C. parviflora*, and *C. Marschallii* are all indigenous in areas widely separated from that of *C. aurea*. For this group of four hybrids the evidence from metaphase pairing is consistent with the evidence from comparative morphology, chromosome number, and geographic distribution of the parent species.

The other six hybrids, all having advanced species for both parents, are consistent, on the whole, with the first four. The first two, however, are probably significantly different with respect to mean number of bivalents, the difference being nearly three times its standard error. Yet the two pairs of species are fairly comparable, *C. tectorum* being somewhat more primitive than *C. Dirosoridis*, and *C. divaricata* certainly more primitive than *C. vesicaria*. In both these hybrids the parent species occur in different areas, but *C. Dirosoridis* and *C. divaricata* are more widely separated geographically than the other two. From the lower meiotic regularity of their hybrid, these two species appear to be less similar genetically than *C. tectorum* and *C. vesicaria*. The last two hybrids, *C. aculeata*-*C. aspera* and *C. aspera*-*C. bursifolia*, also have a significant difference in their mean number of bivalents which is consistent with the fact that the parents of the former belong in the same section and occupy the same area, whereas those of the latter are in different sections and occupy different areas. Finally, the hybrids between *C. nicaeensis* and the two subspecies of *C. setosa* are fully as regular in metaphase pairing as the *C. aculeata*-*C. aspera* hybrid, yet the former involve different sections. Although *C. nicaeensis* is more primitive than *C. setosa*, the two species are generally similar morphologically. This is especially clear when *C. setosa typica* is compared with *C. nicaeensis*, and when habit, type of involucre, and size of heads, florets, and fruits are considered. The chromosomes are of the same four types and for the most part similar in size. The two also occur in the same geographic area. Hence, the high meiotic regularity of these hybrids can be interpreted as indicating a certain degree of genic homology in the two species. In this connection it is noteworthy that in the hybrid *C. setosa* \times *C. biennis* (see p. 16) there was no pairing between the chromosomes of the two species. This indicates that there is much less genic similarity between these two species than between *C. nicaeensis* and *C. setosa*.

Structural hybridity and interspecific relationship.—From the study of meiotic irregularities in interspecific hybrids, evidence has been obtained by Müntzing (1934), Sherman (1946), and Tobgy (1943) that the chromosomes of different species contain homologous segments. This research has been summarized briefly in a preceding chapter (pp. 20-21). The hybrids studied by Tobgy and Sherman were between species of the same section, but the one reported by Müntzing was between two species of different sections. This evidence supports the inference, derived from the study of metaphase pairing in other interspecific hybrids, that some degree of homology exists between the chromosomes of different species.

Thus, the available evidence from cytogenetic research on interspecific hybrids supports the conception that all the species of *Crepis* had a common origin and are still more or less similar in genic constitution.

Summary of genetic criteria.—1) Experiments on interspecific hybridization have yielded evidence of considerable significance bearing on the genetic relationships of fifty-five of the species in this genus. In general, the closer their genetic relationship the more easily can species be crossed and the higher is the vigor and fertility of their hybrids. Such experiments provide a valuable criterion for deter-

mining species relationships, and it is highly desirable that further investigations be made in *Crepis*, especially on those sections and species which have not been cultivated and studied cytologically and genetically.

2) From the evidence on intra- and interspecific hybrids in *Crepis* it can be inferred: (1) that similar gene mutations occur in species belonging to widely separated sections; (2) that some closely related species have the same genic milieu but differ in respect to many individual genes; (3) that there is a similar genic background in all the species investigated.

3) Sufficient work has been done on the cytogenetics of interspecific hybrids to demonstrate the significance of metaphase pairing as an indicator of genic homology between the parent species. In this genus there appears to be positive correlation between wide geographic separation and relatively low genic homology. But the available data on *Crepis* hybrids are not adequate for any generalization about phyletic status and meiotic regularity. There should be several series of hybrids all of which involve a single more primitive species as one parent and an ascending series of species for the other parents. So far as possible both parents should occur in the same region. Such a series might be made up from the tropical African species (sec. 8) or by starting again with *C. leontodontoides* and selecting a series from a number of other sections. Similarly, there is ample opportunity in this genus for further significant studies on structural hybridity and karyotype analysis and their bearing on evolution. But the work thus far accomplished proves the importance of reciprocal translocation as a process of speciation in *Crepis*.

4) All of the genetic evidence supports the conception of a monophyletic origin of the genus as a whole.

INTERSPECIFIC HYBRIDIZATION IN CREPIS

In the data that follow, the female parent is given first. Abbreviations stand for the terms indicated, as follows: r, includes reciprocal cross; a, achenes, including parthenocarpic ones; c, developed only to cotyledon stage; w, weak hybrids; v, vigorous hybrids; h, high fertility; m, medium fertility; mh, medium to high; lf, low fertility; vl, very low fertility; s, sterile; vls, very low or sterile.

A. Diploid species in the same section

- Section 6. *conyzaefolia*—*blattarioides*, 2a, 2c, s.
- Section 9. *leontodontoides*—*suberostris*, r, 24a, 9v, s.
leontodontoides—*tingitana*, 17a, 0.
- Section 10. *latialis*—*chondrilloides*, 13a, 13v, lf.
pannonica—*chondrilloides*, 27a, 21v, vls.
pannonica—*latialis*, 33a, 24v, lf.
pannonica—*Triasii*, 61a, 50w, 3v, s†.
- Section 19. *pulchra*—*palaestina*, r, many a, many v, m.
pulchra—*Reuteriana*, 19a, 11v, vl.
- Section 20. *alpina*—*foetida vulgaris*, r, 43a, 2c, 2w, s.
alpina—*rubra*, r, 40a, 10v, vl.
alpina—*syriaca*, r, 34a, 33v, m.
foetida—*Kotschyana*, 3a, 1w, s.
Kotschyana—*rubra*, 2a, 2v, s.
Kotschyana—*syriaca*, 8a, 8v, vls.
alpina—*Kotschyana*, 1a, 1v, s.
Thomsonii—*foetida* spp., 20 + v, vls-mh.
Thomsonii—*eritreensis*, r, 12a, 12v, h.
eritreensis—*foetida* spp., 30v, vls-mh.
foetida vulgaris—*rubra*, 30a, 26v, lf.
eritreensis—*Kotschyana*, 25v, s.
foetida—*syriaca*, 7a, 3v, lf.
syriaca—*rubra*, 16a, 0.
Thomsonii—*Kotschyana*, 2v, s.

Section 24. *capillaris*—*neglecta*, 44a, 1w, s.
corymbosa—*neglecta*, r, 24a, 7v, vl.
neglecta—*fuliginosa*, r, 100a, 19v, vl.

Section 25. *Noronhaea*—*vesicaria andryaloides*, several v, m.
divaricata—*vesicaria andryaloides*, several v, m.
divaricata—*Noronhaea*, several v, vl.
divaricata—*canariensis*, several v, m.
canariensis—*Noronhaea*, r, several v, vl-lf.
canariensis—*vesicaria* spp., 16v, s-m.
divaricata—*Clausonis*, 42a, 7c, 6v, mh.
Clausonis—*vesicaria myriocephala*, 11a, 3w + 8v, 1m.
Fontiana—*divaricata*, 9a, 8v, m.
Fontiana—*Noronhaea*, 27a, 24v, mh.
Fontiana—*vesicaria taraxacifolia*, 21a, 17w or v, mh.

Section 26. *aculeata*—*aspera*, 83a, 35v, m.
aculeata—*juvenalis*, 18a, 12w, s.
amplexifolia—*aspera*, 44a, 17v, vl.
aspera—*setosa*, 1a, 0.

B. Diploid species in different sections

The more primitive parent is listed first; when the less primitive one was the female it is indicated by ♀.

Sections

1–6. *sibirica*—*conyzaefolia* ♀, 1a, 0.
 1–10. *sibirica*—*pannonica* ♀, 6a, 2c, 1v, s?.
 1–25. *paludosa*—*libyca* ♀, 8a, 1w, s.
 4–6. *chrysantha*—*conyzaefolia* ♀, 3a, 0.
 4–9. *aurca*—*tingitana*, 5a, 3w, s.
 4–9. *aurca*—*leontodontoides*, 24a, 9v, lf.
 4–14. *aurea*—*tectorum*, 8a, 2c.
 4–20. *aurca*—*foetida*, 64a, 0.
 4–20. *aurca*—*rubra*, 32a, 0.
 4–23. *aurea*—*Dioscoridis*, 14a, 0.
 4–24. *aurea*—*capillaris* ♀, 18a, 0.
 4–25. *aurea*—*vesicaria taraxacifolia*, 16a, 3w, s.
 5–10. *Mungierii*—*oporinoides*, 4a, 0.
 5–19. *mollis*—*Reuteriana*, 9a, 0.
 5–25. *montana*—*Clausonis* ♀, 14a, 3w or v, s.
 5–25. *montana*—*libyca*, 4a, 0.
 5–25. *montana*—*vesicaria* spp. ♀, 23a, 16w, s.
 5–25. *Mungierii*—*vesicaria taraxacifolia* ♀, 8a, 7w, s.
 5–25. *Mungierii*—*divaricata* ♀, 23a, 2w, 1v, s.
 6–7. *conyzaefolia*—*albida*, 1a, 0.
 6–8. *blattarioides*—*alpestris*, 22a, 1w, 16v, lf.
 6–10. *conyzaefolia*—*pannonica*, 36a, 15v, vl.
 6–10. *blattarioides*—*pannonica* ♀, 28a, 11w, s.
 6–14. *conyzaefolia*—*Bungei*, 1a, 0.
 7–8. *albida*—*alpestris*, 2a, 1v, vl.
 7–10. *albida*—*pannonica* ♀, 162a, 34c, 62w, s.
 8–9. *alpestris*—*leontodontoides* ♀, 33a, 0.
 9–10. *leontodontoides*—*oporinoides*, 1a, 1w, s?.
 9–14. *leontodontoides*—*tectorum*, 43a, 17c, 12w, vl.
 9–19. *tingitana*—*palaestina* ♀, 12a, 0.
 9–19. *tingitana*—*pulchra* ♀, 4a, 0.
 9–20. *tingitana*—*foetida* ♀, 19a, 0.
 9–20. *leontodontoides*—*foetida*, 43a, 0.
 9–20. *tingitana*—*rubra*, 5a, 0.
 9–23. *tingitana*—*Dioscoridis*, 13a, 0.
 9–23. *leontodontoides*—*Dioscoridis*, 4a, 1c.
 9–24. *leontodontoides*—*nicaeensis*, 42a, 0.
 9–24. *leontodontoides*—*parviflora*, 24a, 7w, 13v, s.
 9–24. *leontodontoides*—*capillaris*, r, 200a, 32w, 89v, s.

Sections

9-24. *leontodontoides*—*neglecta*, 7a, 0.
 9-25. *tingitana*—*libyca*, 5a, 0.
 9-25. *leontodontoides*—*Clausonis*, 41a, 8c, 2v, s.
 9-25. *tingitana*—*vesicaria* spp., r, 49a, 0.
 9-25. *leontodontoides*—*vesicaria* spp., r, 47a, 18w, 10v, vls.
 9-26. *leontodontoides*—*aspera*, 56a, 9c, 25w, s†.
 9-26. *leontodontoides*—*setosa*, 174a, 10c, 3w, 3v, s.
 9-26. *suberostris*—*aculeata* ♀, 19a, 7v, s†.
 9-27. *leontodontoides*—*bursifolia*, 127a, 21c, 46v, s.
 9-27. *leontodontoides*—*senecioides*, 11a, 0.
 10-19. *pannonica*—*pulchra* ♀, 36a, 4c, s.
 10-19. *latialis*—*pulchra* ♀, 5a, 2c, s.
 10-20. *pannonica*—*rubra*, 4a, 0.
 10-20. *pannonica*—*foetida commutata* ♀, 6a, 0.
 10-23. *pannonica*—*patula*, 33a, 29w, lfs†.
 10-23. *pannonica*—*Dioscoridis*, 34a, 9v, s.
 10-23. *oporinoides*—*patula*, 11a, 5w, 5v, s.
 10-25. *pannonica*—*divaricata* ♀, 69a, 0.
 10-25. *pannonica*—*vesicaria* spp., 10a, 2c, s.
 10-25. *oporinoides*—*canariensis* ♀, 57a, 13w, 2v, s.
 10-26. *pannonica*—*aculeata*, 9a, 1w, s†.
 13-19. *praemorsa*—*pulchra* ♀, 17a, 0.
 13-19. *incarnata*—*pulchra* ♀, 16a, 0.
 13-25. *incarnata*—*vesicaria myriocephala* ♀, 0.
 13-26. *incarnata*—*setosa*, 1a, 0.
 14-19. *tectorum*—*pulchra* ♀, 27a, 0.
 14-24. *tectorum*—*nicaeensis* ♀, 14a, 6c, 3w, 4v, s.
 14-24. *tectorum*—*capillaris* ♀, 117a, 88c, 22v, vls.
 14-25. *tectorum*—*Clausonis* ♀, 7a, 1c, 1v, s.
 14-25. *tectorum*—*divaricata* ♀, 16a, 13v, vl.
 14-25. *tectorum*—*libyca* ♀, 3a, 3c, s.
 14-25. *tectorum*—*vesicaria taraxacifolia* ♀, 70a, 14c, 39w + v, vls.
 14-26. *tectorum*—*amplexifolia*, 5a, 2c, s.
 14-26. *tectorum*—*aspera*, r, 20a, 1w, 10v, vls.
 14-26. *tectorum*—*setosa*, 30a, 10v, vl.
 14-27. *tectorum*—*bursifolia*, r, 22a, 12c, 1w, s.
 19-20. *palaestina*—*rubra*, 22a, 0.
 19-20. *palaestina*—*foetida*, 7a, 0.
 19-23. *palaestina*—*Dioscoridis*, 2a, 0.
 19-23. *pulchra*—*Dioscoridis*, 269a, 4c, 1w, s.
 19-25. *pulchra*—*Clausonis*, 2a, 0.
 19-25. *pulchra*—*divaricata*, 4a, 2c, 2w, s.
 19-25. *pulchra*—*vesicaria myriocephala* ♀, many a, 0.
 19-25. *palaestina*—*vesicaria taraxacifolia*, r, 22a, 5w, s.
 19-26. *pulchra*—*aculeata*, 10a, 0.
 20-24. *syriaca*—*capillaris* ♀, 2a, 0.
 20-24. *foetida*—*neglecta* ♀, 2a, 0.
 20-25. *Kotschyana*—*libyca*, 2a, 1v, vl.
 20-25. *Kotschyana*—*vesicaria taraxacifolia*, 15a, 0.
 20-25. *rubra*—*Clausonis* ♀, 11a, 0.
 20-25. *rubra*—*vesicaria myriocephala*, 32a, 0.
 20-26. *rubra*—*amplexifolia* ♀, 5a, 0.
 20-26. *rubra*—*setosa*, r, 32a, 2w, s.
 23-24. *Dioscoridis typica*—*neglecta*, 1a, 1c.
 23-25. *Dioscoridis typica*—*Clausonis* ♀, 21a, 1v, s.
 23-25. *Dioscoridis typica*—*divaricata* ♀, 63a, 8c, 1w, s.
 23-25. *Dioscoridis typica*—*vesicaria* 2 spp. ♀, 69a, 8c, 3w, s.
 23-26. *Dioscoridis typica*—*aculeata* ♀, 44a, 7c, 18v, vls.
 23-26. *Dioscoridis typica*—*aspera*, r, 61a, 6v, vl.
 23-26. *Dioscoridis typica*—*setosa* ♀, 6a, 0.
 24-25. *capillaris*—*Clausonis* ♀, 12a, 1w, 5v, s.

Sections

24–25. *capillaris*—*vesicaria taraxacifolia*, 2a, 1v, vl.
 24–25. *parviflora*—*Clausonis* ♀, 9a, 3w, 3v, s.
 24–25. *neglecta*—*vesicaria taraxacifolia* ♀, 29a, 0.
 24–26. *nicaeensis*—*setosa*, 81a, 6c, 2v, vl.
 24–26. *parviflora*—*setosa* ♀, 1a, 0.
 24–26. *capillaris*—*aculeata* ♀, 15a, 2c, 2w, 5v, vl.
 24–26. *capillaris*—*aspera*, 81a, 3w, 24v, vl.
 24–26. *capillaris*—*setosa*, 16a, 8w, vl.
 24–27. *capillaris*—*bursifolia*, 29a, 12w, vls.
 24–27. *parviflora*—*bursifolia*, 10a, 1v, vls.
 24–27. *neglecta*—*bursifolia*, 6a, 3w, s.
 24–27. *parviflora*—*senecioides* ♀, 28a, 1w, 8v, s.
 25–26. *Clausonis*—*aspera*, 12a, 3c, 5v, vl.
 25–26. *Clausonis*—*setosa*, 3a, 0.
 25–26. *divaricata*—*amplexifolia*, 5a, 1v, lf.
 25–26. *divaricata*—*aspera*, 43a, 26w, 5v, vl.
 25–26. *vesicaria* 3 spp.—*amplexifolia*, 59a, 34v, lf.
 25–26. *vesicaria* 4 spp.—*aspera*, 124a, 6w, 68v, vl.
 25–26. *vesicaria* 2 spp.—*setosa*, 18a, 1w, 15v, vls.
 25–27. *Clausonis*—*bursifolia*, 43a, 6c, 26w, 8v, lf.
 25–27. *divaricata*—*bursifolia*, 2a, 0.
 25–27. *vesicaria* 4 spp.—*bursifolia*, 137a, 27c, 82v, lf.
 25–27. *vesicaria taraxacifolia*—*senecioides* ♀, 17a, 3v, s.
 26–27. *aculeata*—*bursifolia*, 9a, 7v, vl.
 26–27. *aspera*—*bursifolia*, 2a, 2v, vl.
 26–27. *setosa*—*bursifolia* ♀, 1a, 0.

C. One species polyploid—both in the same section

Section 10. *pannonica*—biennis, r, many a, 0.

Section 25. *Clausonis*—*vesicaria taraxacifolia* 4n form ♀, 2a, 1c.

canariensis—*vesicaria taraxacifolia* 4n form, r, 21a, 11w, s.

divaricata—*vesicaria taraxacifolia* 4n form, 64a, 11v, lf.

vesicaria taraxacifolia—*vesicaria taraxacifolia* 4n form, 109a, 6w, 50v, lf.

D. One species polyploid—the two in different sections

Sections

4–10. *aurea*—biennis, 11a, 0.
 4–11. *chrysantha*—*crocea* ♀, 2a, 0.
 9–25. *leontodontoides*—*vesicaria taraxacifolia* 4n form, 1a, 1v, s.
 10–11. *chondrilloides*—*crocea*, 15a, 0.
 10–13. *biennis*—*incarnata* ♀, 1a, 0.
 10–19. *biennis*—*palaestina* ♀, 2a, 0.
 10–19. *biennis*—*pulchra* ♀, 5a, 0.
 10–20. *biennis*—*rubra*, r, 10a, 1w, 4v, s.
 10–20. *biennis*—*foetida*, 1a, 1v, s.
 10–23. *biennis*—*Dioscoridis*, 4a, 0.
 10–24. *biennis*—*nicaeensis*, 45a, 1w, s.
 10–24. *biennis*—*parviflora* ♀, 37a, 6v, lf.
 10–24. *biennis*—*capillaris* ♀, 28a, 0.
 10–24. *biennis*—*neglecta* ♀, 23a, 0.
 10–25. *biennis*—*vesicaria* 4 spp. ♀, 95a, 0.
 10–26. *biennis*—*setosa*, 6a, 1 or more v, lf.
 10–27. *biennis*—*senecioides* ♀, 35a, 0.
 11–14. *crocea*—*Bungei*, 2a, 2v, lf.
 11–18. *crocea*—*pulchra* ♀, 35a, 0.
 23–25. *Dioscoridis*—*vesicaria taraxacifolia* 4n form, 3a, 1c, 1v, s.

E. Both species polyploid

Sections

10. *ciliata*—biennis, 8a, 1w, 4v, mh.
 10–25. *biennis*—*vesicaria taraxacifolia* 4n form, 1a, 0.

CHAPTER 4

THE PHYLOGENY OF CREPIS

THE GENERIC RELATIONSHIPS OF CREPIS

EXCEPT FOR one other genus, *Crepis* is the largest in the tribe Cichorieae of the family Compositae, the exception being *Hieracium*. This tribe, which is characterized by the presence of milky juice, the ligulate corollas, and the perfect, usually monomorphic, flowers, is the most natural one in the entire family; but within the tribe the relationships of the genera are very complex and no system exists which has successfully divided it into subtribes. As a first step toward a critical revision of this tribe, Stebbins (unpublished) has prepared a tentative reclassification of the sixty-four genera in the group, based on preliminary studies of comparative morphology, geographic distribution, and chromosome numbers, from which he has kindly permitted me to use such parts as are basic to the present discussion. Stebbins recognizes eight subtribes as follows: (1) Scolyminae, one genus with basic chromosome number $x = 5$ or 10; (2) Cichorinae, four genera with basic chromosome number $x = 9$; (3) Microseridinae, eight genera with basic chromosome numbers $x = 9, 6$, and 5; (4) Stephanomerinae, eleven genera with basic chromosome numbers $x = 9, 8$, and 7; (5) Dendroseridinae, one genus with basic chromosome number $x = 9$ or 18; (6) Scorzonerinae, three genera with basic chromosome numbers $x = 7$ and 6; (7) Leontodontinae, nine genera with basic chromosome numbers chiefly $x = 7, 6, 5$, and 4; (8) Crepidinae, twenty-seven genera with basic chromosome numbers $x = 9$ and 8, except in *Crepis*, which has $x = 6, 5, 4$, and 3, and in one exceptional section $x = 7$.

Subtribe Crepidinae, according to Stebbins, is a very diverse group, but with close affinities and often complex interrelationships connecting the genera. All the genera seem to have diverged from a common stock, which formed branches or meshes which are still represented by modern genera. The end members of these lines are widely divergent, but the basic genera show close affinities. The genus *Dubyaea* (cf. Stebbins, 1940) is definitely the most primitive genus of the subtribe, and its ancestral stock, which was probably larger and more diverse than the present relict genus, may be taken as the starting point for each of these lines. The five lines, designated by naming the genus nearest to *Dubyaea* first and the most divergent or specialized genus second, are as follows: (1) *Hieracium-Tolpis*, (2) *Launaea-Sonchus*, (3) *Prenanthes-Lactuca*, (4) *Youngia-Ixeris*, (5) *Crepis*.

The *Crepis* line consists of that genus alone, but it contains about as many species as any except perhaps the *Hieracium-Tolpis* line. It shows no direct connections with any species of *Dubyaea*, although the most primitive species of *Crepis* do exhibit resemblances in one character to one species of *Dubyaea* and in other characters to others (cf. pp. 64-65). The *Crepis* line is the only line that does not have the primitive basic chromosome numbers $x = 9$ and $x = 8$, which are the only ones known in *Dubyaea*. That the *Crepis* line is not derived from any known members of any other line is evident from two facts: (1) none of the primitive species of *Crepis* resembles the primitive members of any other line more than one would expect in members of the same subtribe; (2) the floral anatomy of such species as *Crepis geracioides* shows features more primitive than those known in any other genus of the Crepidinae except *Dubyaea*. On the other hand, *Crepis* resembles the Leontodontinae in habit, floral characteristics, and achenes more closely than does any other genus of the Crepidinae. For this reason the similarity in chromosome

number and karyotype which exists between *Crepis* and the Leontodontinae may be evidence of actual relationship as well as parallel evolution.

It is assumed by Stebbins, therefore, that *Crepis* arose from certain primitive, now extinct, species of *Dubyaea*, which were related fairly closely to the ancestors of the Leontodontinae. The degree of diversity found even in the primitive species of *Crepis* makes it necessary to assume that the different lines and groups now existing in the genus were derived from fairly numerous but interrelated ancestral species. Some of these ancestors must have had 14 and some 16 chromosomes; and the karyotypic differences between all the species of *Crepis* and *Dubyaea* (Babcock, Stebbins, and Jenkins, 1937, p. 194, fig. 2) are so marked that structural differentiation of the chromosomes must have been going on more actively in this ancestral stock than in the progenitors of any other line of the Crepidinae.

Among other lines of the Crepidinae, *Crepis* is most similar to the *Youngia-Ixeris* line. The resemblances between these two lines seem to become less rather than greater when their more primitive species are compared. Therefore, it seems possible that their resemblances are due to the origin of the two lines from similar species of *Dubyaea* and to parallel evolution, rather than to an actual close relationship in recent times. In fact, there are good reasons for considering the *Hieracium-Tolpis* line to be as closely related to *Crepis* as the *Youngia-Ixeris* line. In *Hieracium* are found plants remarkably similar to *Crepis* in habit, involucres, and flowers and sometimes even in their fruits. The terete achenes with equal ribs are characteristic of *Hieracium* and *Tolpis*, but are found in only a few species of the *Youngia-Ixeris* line, chiefly in *Ixeris* subg. *Crepidiastrum* (Nakai) Stebbins (1937a, p. 45) and in the primitive species of *Chondrilla*.

The greatest concentration of both primitive and advanced species of *Crepis* is at present in western Eurasia. This fact, along with the fact that the related Leontodontinae and the *Hieracium-Tolpis* line are predominantly European, was considered by Stebbins to indicate that *Crepis* originated in western Eurasia. This agrees with the hypothesis that the *Dubyaea* ancestors of *Crepis* are now extinct. These ancestors can be assumed to have existed, probably in the early part of the Tertiary period, in western Eurasia, with their relatives, the ancestors of the Leontodontinae and the *Hieracium-Tolpis* and *Launaea-Sonchus* lines. The great orographic and climatic changes which western Eurasia has undergone since early Tertiary times, along with competition with their very numerous and efficient descendants, could easily account for the complete extinction of these ancestors. One living relative, *Dubyaea oligocephala*, occurs in south Central Asia, but in a region which contains many western Eurasian types, such as the genus *Cedrus*. It is recognized by Stebbins, however, that *Crepis* does not show so great a concentration of primitive types in Europe as do the other groups mentioned and that, therefore, some of its ancestors at least may have originated in Asia. The present author's deductions from his detailed study of the distribution of *Crepis* are presented in chapter 5.

THE SECTIONS OF CREPIS AND THEIR INTERRELATIONSHIPS

The twenty-seven sections of *Crepis* recognized in this monograph fall naturally into three main phyletic groups. These groups, however, cannot be distinguished from one another by a sufficient number of constant differences to warrant their establishment as subgenera. They are used here merely as a basis for the discussion of interrelationships. The numerical order of the groups and sections, as well as the species in each section, indicates as nearly as possible in a linear series their relative primitiveness or advancement. Table 4 gives the sections in each group, together with the number of perennial or shorter-lived species in each section.

Group I, with its seven sections and twenty-nine species, considered as a whole, is the most primitive of the three groups on the basis of both morphological and cytological evidence. (1) Morphologically, *Crepis sibirica*, *C. geracioides*, and *C. kash-*

TABLE 4
THE SECTIONS OF CREPIS ARRANGED IN PHYLETIC GROUPS

Section	Number of species	Basic chromosome numbers	Number of perennial species	Biennial or annual species
<i>Group I. The rhizomatous species</i>				
1. Desiphylion.....	4	6, 5	4	..
2. Spathoides.....	1	6	1	..
3. Omaloclina.....	1	6	1	..
4. Brachypodes.....	9	6, 5, 4	9	..
5. Mesomeris.....	8	6	8	..
13. Intybellia.....	3	4	3	..
21. Microcephalum.....	4	5	4	..
<i>Group II. The more primitive taprooted species</i>				
6. Soyeria.....	3	5, 4	3	..
7. Paleya.....	3	5	3	..
8. Anisoramphus.....	26	4	26	..
9. Gephyroides.....	3	5	2	1
10. Berinca.....	29	5, 4	27	2
11. Macropodes.....	14	5, 4	14	..
12. Ixeridopsis.....	7	7	7	..
14. Mesophylion.....	3	4	2	1
15. Psilocheania.....	10	11	10	..
16. Lagoseris.....	5	?	5	..
17. Napiseris.....	1	?	1	..
18. Pyrimachos.....	5	?	5	..
<i>Group III. The more advanced taprooted species</i>				
19. Phaeacium.....	6	4	1	5
20. Hostia.....	9	5, 4	..	9
22. Pterotheca.....	1	5	..	1
23. Zacintha.....	4	4, 3	1	3
24. Phytodesia.....	10	4, 3	..	10
25. Lepidoseris.....	13	4	9*	4*
26. Nemauchenes.....	7	4	..	7
27. Psammoseris.....	7	4	4	3

* These species are variable with respect to the length of life of the individual plant.

mirica, the most primitive species in the genus, show more resemblance to *Dubyaea*, the most primitive genus in the subtribe Crepidinae, than do any other species of *Crepis*. Although none of the existing species of *Dubyaea* shows close resemblance to any *Crepis* species, yet *C. sibirica* and *C. geracioides* do show resemblance to *D. atropurpurea* and *D. oligocephala* in the lyrate leaves, to *D. oligocephala* in the shape and unequal ribbing of the achenes, and to *D. hispida* in the calyculate,

setose involucres. *C. kashmirica*, on the other hand, shows resemblance to *D. chimi-liensis* in habit and leaf shape, to *D. hispida* in involucral characters, to *D. oligocephala* in floral characters, and to *D. atropurpurea* to some extent in the shape and ribbing of the achenes. Furthermore, the large size of the basal leaves, the leafy stem, and the few large heads are common features of all of these species. (2) Karyologically, sections 1–5 are considered the most primitive groups of *Crepis*; this is because these sections are the only ones containing 6-paired species, some of which, *C. kashmirica* and *C. terglouensis*, have the most symmetrical chromosomes of all *Crepis* species. (3) Reduction in length of the life cycle has accompanied morphological reduction and specialization in this genus. It will be noted in table 4 that all the species in Group I and all but four in Group II are perennial, whereas about three-fourths of the species in Group III are biennial or annual. Actually, nearly all of the forty-two species in this last column under Group III are annuals and many of these are precocious and ephemeral.

Although the most primitive species of *Crepis* have a rhizome instead of a true root, yet several taprooted species in sections 6–10, with 5 and 4 pairs of chromosomes, are also very primitive types. There is considerable evidence in *Crepis*, especially the obvious close relationship between sections 4, 9, and 14 and between sections 13 and 19, discussed below, that the taprooted type was derived from the rhizomatous type. At least one species of *Dubyaea* [cf. *D. tsarangensis* (W. W. Smith) Stebbins] has strong, fleshy surface roots instead of a true taproot; and similar fleshy, fibrous roots are found in *Prenanthes sinensis* (Hemsl.) Stebbins. Some species of *Youngia* and *Ixeris* are also characterized by having a rhizome. It seems justifiable, therefore, to assume that the ancestors of *Crepis* as well as the existing species of *Dubyaea* were rhizomatous. Such an assumption is consistent with the conception that *Dubyaea* had its early development in a temperate climate at low elevations and under moist conditions, all of which conditions probably existed in Central Asia in late Oligocene and early Miocene time (see Appendix 1, p. 157). Unfortunately, observations on the seedling root systems of the primitive rhizomatous species have not been reported. If the young seedlings of such species also have root systems resembling those of taprooted species, invocation of the biogenetic law would seem fully warranted. In other words, the taproot may have been characteristic of the more remote ancestors of *Crepis*, whereas the rhizome evolved in the immediate ancestors of *Crepis* through mutations favoring adaptation to a more moist environment. Furthermore, the occurrence of the taproot in the more advanced species of the genus can be explained as the result of mutations favoring persistence of the seedling root and suppression of the rhizome accompanying gradual adaptation to a more xeric environment.

With reference to the chromosomes, it may be assumed that, in the *Dubyaea*-like ancestors of *Crepis*, reduction in number from 8 to 7, 6, or 5 had already occurred.

The seven sections in Group I fall into two subgroups on the basis of relative degree of primitiveness. Sections 1–5 are all primitive morphologically, whereas sections 13 and 21 are more advanced. On the basis of degree of resemblance, however, sections 1, *Desiphylion*, and 5, *Mesomeris*, are closer to each other than to the other five. The more primitive species in section 5, like all those in section 1, have a strong horizontal or oblique rhizome and tall leafy stems; but in the more advanced species of section 5 the rhizome is praemorse, as in section 4, and the stems shorter, more slender, and with smaller leaves. Types of involucre, flowers, and fruits are in general agreement with this statement.

Crepis kashmirica (sec. 2) has one of the two most primitive karyotypes in the genus, the other being that of *C. terglouensis*. Except that the leaves are not at all

lyrate and the florets are somewhat smaller than one might expect in such a primitive species, *C. kashmirica* could pass as a member of section 1. It has the most prominently ribbed achenes of all the species in the genus, this being a characteristic of other primitive species, such as *C. sibirica*, *C. pygmaea*, *C. terglouensis*, and *C. pontana*. It is also noteworthy that in *C. kashmirica* the marginal achenes are sometimes parthenocarpic and that these seedless fruits strongly resemble typical achenes of *Youngia* species in shape and ribbing. Normal marginal achenes of *C. kashmirica* retain this resemblance to some extent. Hence, this species appears to be a primitive relic in which the florets have become considerably reduced in size. This phenomenon of marked reduction in one or two organs or parts in otherwise primitive endemic species occurs elsewhere in the genus, most notably in *C. patula*.

In the single species in section 3, *Crepis pygmaea*, the plant spreads by stolons, often developing long subterranean stems. The flowering stems and leaves are much reduced. Evidently this species has become especially adapted to the peculiar conditions obtaining on the loose, gravelly soils of steep mountain slopes. At the same time, the strongly ribbed achenes are very primitive, especially in subsp. *anachoretica*, in which the ribs are alternately wide and narrow. The species exhibits strong resemblances in the leaves, in both adult and seedling stages, as well as in its achenes, to *Youngia depressa* (Hook. f. et Thoms.) Babc. et Stebbins (1936), which is the most primitive species in that genus. In its tufted habit, spatulate leaves, and short, thick, strongly ribbed achenes, *C. pygmaea* also shows marked resemblance to *Soroseris umbrella* (Franch.) Stebbins (1940), which is considered by Stebbins as forming a connecting link between *Soroseris*, *Youngia*, and *Dubyaea*. These definite indications of genetic relationship between one of the most primitive *Crepis* species and the most primitive species in both *Soroseris* and *Youngia*, and between all three of these genera and *Dubyaea*, is of special importance in connection with the problem of the region of origin and early development of *Crepis*.

Brachypodes, section 4, must also be considered as a primordial derivative from the original *Crepis* stock. The most primitive species, *C. terglouensis*, has the tufted habit and short, thick, strongly ribbed achenes which are common to *C. pygmaea* and its relatives in *Youngia* and *Soroseris*; but its leaves are lanceolate and pinnatifid and the involucre is definitely more primitive than in *C. pygmaea*. The 6 pairs of chromosomes also comprise a more primitive karyotype than that of *C. pygmaea*. It is especially noteworthy that in all the species of this section the stems are scapiform in contrast with the strongly branched, leafy stem characterizing the species in the other most primitive sections (in *C. pygmaea* the stem, although short, is usually branched). Thus, it appears that this section arose from a different *Dubyaea* type from the one that produced sections 1, 2, 3, and 5. It is highly probable that this *Dubyaea* type had already become adapted to alpine conditions.

Intybellia (sec. 13) and *Microcephalum* (sec. 21) are comprised of more advanced species; but in each the praemorse rhizome indicates a phylogenetic connection with the more primitive sections of this group. Since in each species the stem is more or less branched, forming a cymose or racemose inflorescence, these sections were probably derived from the 1-5 line rather than the 4 line.

The relationships of these sections to each other and to the other sections of the genus are shown in figures 3 and 4. The distribution of all the sections will be discussed in the following chapter.

Group II, containing twelve sections and 110 species, is much the largest of the three groups. For the first six sections (6-11) and another (14) the phylogenetic connections appear to be very certain. For the rest (secs. 12 and 15-18) they are more hypothetical but for the most part, it is believed, fairly dependable.

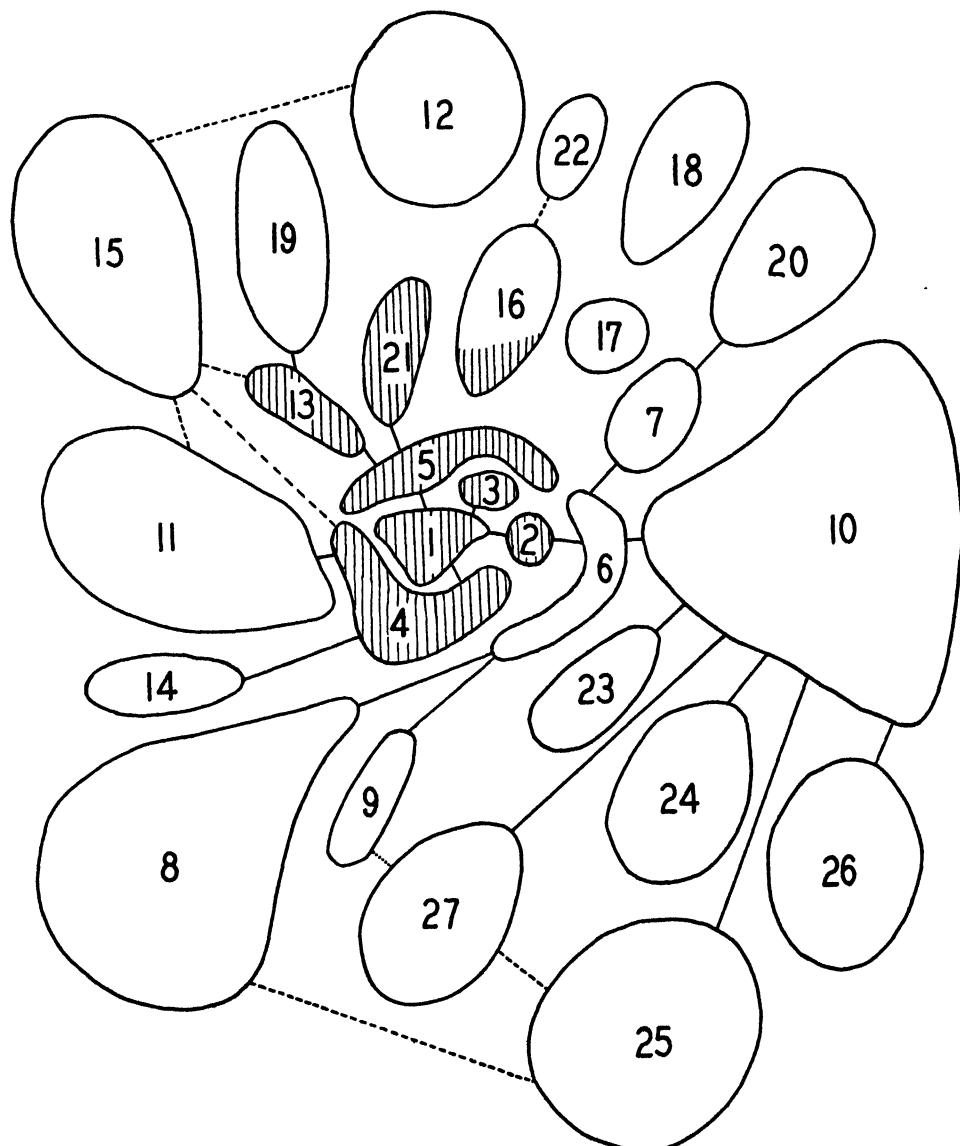


Fig. 3. Cross-sectional chart showing present-day interrelationships of the sections of *Crepis*. Shaded sections contain the rhizomatous species. The lines joining certain sections indicate assumed earlier connections, the solid ones showing more definite relationships than the broken ones. The phylogenetic relationships between the sections are not and cannot be adequately shown in this diagram.

Section 6 contains the most primitive 5-paired species in the genus (except *C. sibirica*), viz., *C. pontana*, which, except for the deep-rooted habit and the non-lyrate leaves, could pass as a member of section 1. The leaves of *C. pontana*, like those of the other species in this section, resemble the leaves of *C. kashmirica* more than those of any other primitive species. Although the species of section 6 are characterized by a deeply penetrating taproot; yet in one of them (*C. blattarioides*) the upper part of the root is often thick, sometimes horizontal, and always strongly

fibrous. These peculiarities certainly suggest a derivation from a rhizomatous type. Thus, it seems highly probable that section 6 was derived from the same line that produced *C. kashmirica*. The most primitive 4-paired species in the genus are *C. conyzaeifolia* and *C. blattarioides*. Morphologically they are fairly close to *C. pontana*, though more reduced, and the karyotype of *C. conyzaeifolia* is somewhat similar to that of *C. pontana*. Both *C. pontana* and *C. blattarioides* are relic species of the Alps, in contrast with *C. conyzaeifolia*, which extends from the Pyrenees to the Altai.

Sections 7 and 9 are small but very interesting groups believed to have been derived from the 2-6 line (fig. 4). Each contains one more primitive species, *C. albida* of section 7 and *C. tingitana* of section 9. In both sections, also, the most primitive species occurs in both Spain and Morocco. But there the similarity ceases, since the distribution of the other two species is different in the two sections, and morphologically *C. albida* and *C. tingitana* are very different, although both have $n = 5$ chromosomes. *C. albida* exhibits definite affinity with *C. alpina* of section 20 but is a much more primitive species, whereas *C. tingitana* shows some resemblance in type of root and achenes to section 8. It should be noted that *C. leontodontoides*, also of section 9, provides further important evidence for the derivation of the taproot type from the rhizome type in *Crepis*. With respect to root, this species is actually variable, some plants being deep-rooted and some shallow-rooted. Furthermore, F_1 hybrids between *C. leontodontoides* and *C. aurea* of section 4 were found by Avery (1930) to exhibit almost perfect premeiotic chromosome pairing, which certainly indicates close genetic relationship between the two species. Thus, *Gephyroides* (little bridge) is a very appropriate name for section 9.

Sections 8 and 10, the two largest sections in the genus, were apparently derived from section 6 or from the 2-6 line. The connection of section 8 with section 6 is obviously through *C. alpestris* of section 8 and *C. conyzaeifolia* of section 6, since these two species are morphologically certainly fairly close. Furthermore, the karyotype of *C. alpestris* of section 8 is similar to that of *C. blattarioides* of section 6. Although the connection between section 10 and section 6 is less obvious, yet it can hardly be less certain when all the evidence is considered. The four most primitive species in section 10, on the basis of the large size of the plant and all its parts, are little known endemics from the mountains of eastern Turkestan, western Persia, and the eastern end of the Caucasus region in southern Daghestan. Their chromosomes have not been seen, but they probably have either 5 or 4 pairs. Fairly close to them morphologically are the three diploid species, *C. pannonica*, *C. latialis*, and *C. chondrilloides*, each of which has $n = 4$ chromosomes and a karyotype very similar to that of *C. conyzaeifolia*. At the same time, the most primitive species in another subgroup of section 10, *C. Baldaccii*, has a karyotype resembling that of *C. pontana*, the most primitive species of section 6. Furthermore, the evidence from geographic distribution in both section 10 and section 8 is wholly consistent with the assumption that these two large sections were derived from the 2-6 line.

Section 11 contains fourteen species with mostly low scapiform stems and dentate or pinnatifid basal leaves. Except for the deeply penetrating taproot, these plants show more resemblance to the species of section 4 than to any other section; and there are some indications that they have been derived from rhizomatous ancestors. Thus, in *C. bithynica* and *C. Robertioides* numerous fleshy fibers are sometimes present just below the caudex, a feature characteristic of a praemorse rhizome; and

Fig. 4. Phylogenetic relations of the sections of *Crepis*. Large numerals are section numbers and small numerals are basic chromosome numbers. Shaded sections contain the rhizomatous species. Sizes of the circles are roughly proportional to the number of species in the sections. Connections shown by broken or dotted lines are less definitely indicated by the morphological evidence than those shown by solid lines.

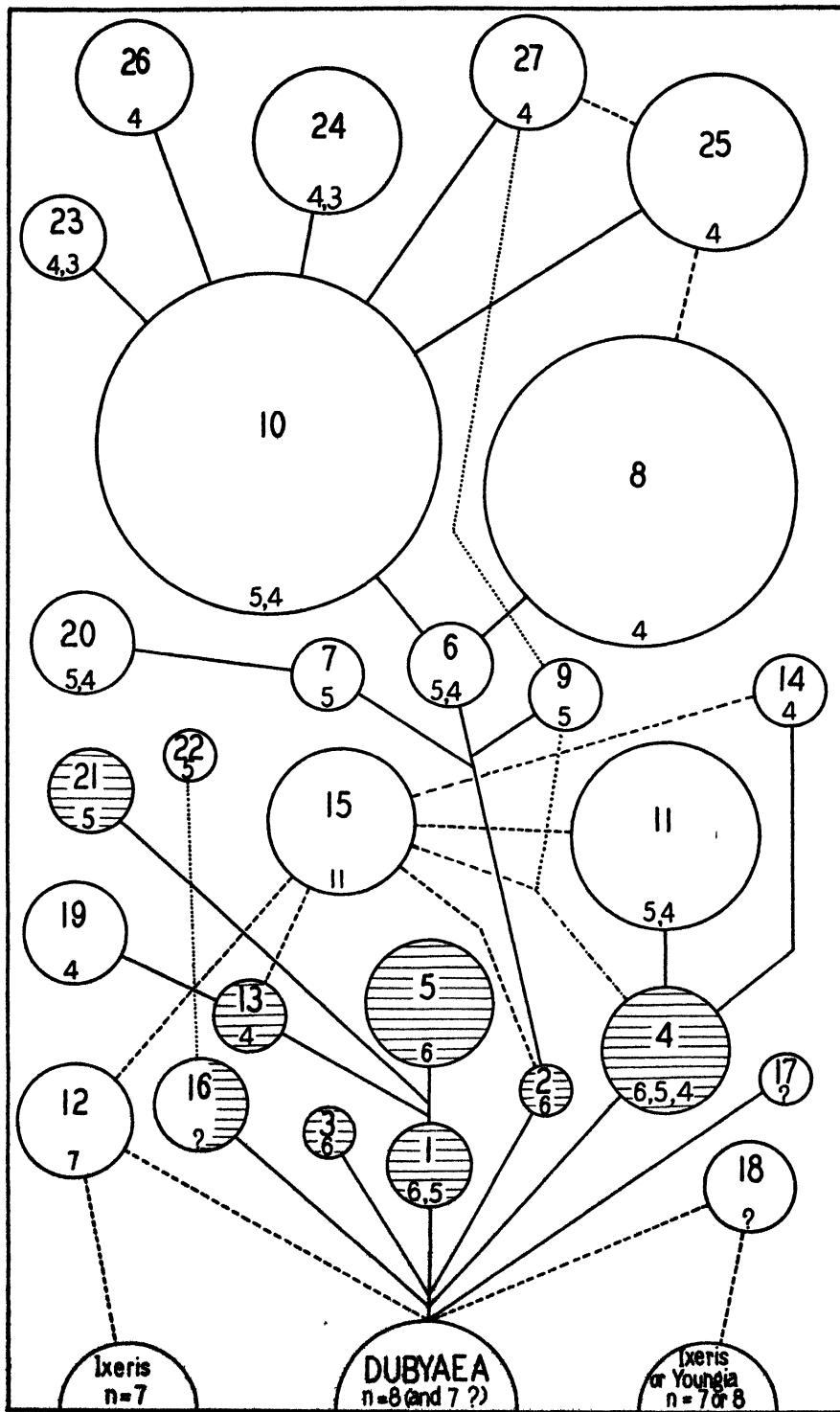


Fig. 4. (For explanation of figure, see bottom of facing page.)

in *C. crocea* and *C. Faureiana* the caudex is swollen and the taproot very slender. Furthermore, the involucre and achenes of *C. Schachtii*, the most primitive species of section 11, resemble those of *C. Jaquinii*, *C. aurea*, and *C. chrysanthia* of section 4. The geographic distributions of the two sections are consistent with the assumption that they represent the same phylogenetic line.

Mesophylion, section 14, consists of three closely related species, the well-known *C. Bungei* and *C. tectorum*, and the very little-known *C. ircutensis*. *C. Bungei*, a perennial species, grows in southern Siberia, where it forms mats in swamps or moist meadows and on riverbanks. This mat-forming habit is made possible by the branching of the very slender roots and by the forming of adventitious buds. Morphologically, *C. Bungei* strongly resembles *C. chrysanthia*, which has a praemorse rhizome, but does not form mats. *C. Bungei* also has a several-headed stem, and the involucres are more reduced and somewhat specialized. But, aside from these differences, the resemblances are truly striking in the leaves, in the involucral bracts, in the florets, especially in the purplish-brown achenes, in the white, 2-seriate pappus with unequal, persistent setae, and even in the areolate receptacle with short, fine cilia scattered on the interspaces, a rather unusual feature in *Crepis* (cf. figs. 28 and 164). Furthermore, the karyotypes of *C. Bungei* and *C. chrysanthia* are almost identical. Thus, it appears certain that section 14 was derived directly from *C. chrysanthia* of section 4 and that we find here further evidence of the derivation of the taproot type from the rhizome type. The similarity in morphology extends to *C. ircutensis* and *C. tectorum* and the latter's karyotype is also closely similar. Hence, its inclusion in this section, even though it has become a widespread, aggressive annual, is fully justified. Mesophylion is certainly an intermediate group, as the name implies, with definite primitive connections and certain advanced aspects (cf. fig. 4).

Considering the other five sections in Group II, we find that each one presents its own peculiar problem. Since none of them throws any light on the main problem of phylogeny within the genus as a whole, they will be discussed very briefly here, leaving consideration of the detailed evidence for the individual sections. Taking them up in numerical order, the origin of Ixeridopsis (sec. 12), the only section with the haploid number 7, can be most reasonably explained through intergeneric hybridization between certain now-extinct *Crepis* species and such 7-paired *Ixeris* species as *I. alpicola*, which exhibits considerable resemblance to *Crepis elegans*. This hypothetical origin of section 12 was first suggested by Babcock, Stebbins, and Jenkins (1937), who pointed out that this hypothesis is more satisfactory from the point of view of the present geographic distribution of the two genera than the hypothesis that section 12 represents the link through which *Ixeris* has been derived from *Crepis* or vice versa (see fig. 4, lower left). The evidence in support of this hypothesis is discussed under section 12 (Part II, p. 528).

Psilocheenia, section 15, comprises all the indigenous American species except *C. nana* and *C. flexuosa*. Like Ixeridopsis, this section is unique with respect to chromosome numbers, all the species in the section being polyploids, with the base number $x = 11$. The probable origin of all the 22-chromosome American species through hybridization of 7- and 4-paired or 6- and 5-paired diploid Asiatic species, followed by amphidiploidy and migration of the new species into North America, where further hybridization, together with polyploidy and apomixis occurred, has been fully discussed by Babcock and Stebbins (1938). The evidence is summarized under section 15 (Part II, p. 572). It should be noted here that sufficient morphological resemblance has been found between some of these American species and certain species of sections 2, 4, 11, 12, 13, and 14 to warrant the assumption that

the diploid ancestors of section 15 belonged to or figured in the ancestry of all those sections. The assumed relationship of section 15 to the other sections mentioned is represented in figure 4 by broken lines.

The remaining three sections in Group II are the only ones in the genus which have not been brought under cultivation and examined cytologically. Each is a unique group in certain aspects. *Lagoseris* (sec. 16) contains five perennial species, all with setiform paleae on the receptacle. Two of these species are endemic in western Persia, two in eastern Asia Minor, and one in Crimea. The only other *Crepis* species with such paleae is *C. sancta* (sec. 22, Group III), a widespread, polymorphic annual. This species, although greatly reduced and specialized, particularly in its desert forms, may have been derived from the same line that gave rise to the five species in section 16. At least one of these species, *C. purpurea*, is rhizomatous; and another one, *C. frigida*, spreads by stolons. Hence, it is assumed that this section arose from the same group of closely related *Dubyaea* species that produced sections 1–5. From the general appearance of the plants it seems likely that most of the *Lagoseris* species have either 5 or 4 pairs of chromosomes, although *C. connexa*, judging from the large size of its pollen grains, might have 6 pairs.

Crepis napifera is an anomalous species the features and relationships of which are considered in detail under section 17. The evidence at present available indicates that it originated from a primitive stock of *Dubyaea* which was probably the ancestral stock of both *Crepis* and *Youngia*.

The last section in Group II, *Pyrimachos*, contains five species which are distinct from all other *Crepis* species, as well as from *Ixeris* and *Youngia*, in the nearly leafless caudex and the peculiarity of having the leaves on the lower part of the stem represented by small, scalelike organs. The small, few-flowered heads and the achenes, although generally *Crepis*-like, show some resemblances to those of both *Youngia* and *Ixeris*. But, for reasons stated in the discussion of this section (Part II, p. 634), it is concluded that these species must be included in *Crepis*, although they show definite affinity with *Youngia*. It is possible that they originated from a common ancestral stock or that, like section 12, they resulted from intergeneric hybridization between *Crepis* and both *Youngia* and *Ixeris* at a time when these genera were not strongly differentiated from one another. The latter hypothesis is indicated in figure 4, lower right.

Group III contains eight sections and fifty-seven species. More than half of these species are annuals and several are aggressive, with wide distributions. Along with this marked evidence of advancement in evolution has gone more or less reduction in size of the plant and all its parts; also, a certain degree of parallelism in karyotype modification has taken place. That these progressive changes have not been confined to one or two lines but are general within the genus is evident from the fact that these advanced sections are so numerous and that they are so distinct from one another. This is another argument supporting the conception of the close genetic relationships within the genus as a whole.

Phaeacium, section 19, with six species, has been mentioned (p. 43) as providing evidence that taprooted groups have originated from rhizomatous ancestors. This evidence is found in the one perennial species of this section, *C. Reuteriana*, which is polymorphic. In both subspecies the rootlike, subterranean stem is strongly woody and elongated, sometimes horizontally; at the same time it is usually swollen at the top, and the upper part always bears many strong lateral roots resembling the fibers produced on true rhizomes. This peculiar structure of the underground part of the plant strongly suggests the derivation of this species from a rhizomatous ancestor. It is significant that the karyotypes of the species in this section and

in section 13 are indistinguishable. This indication of relationship between the two sections is supported by a certain amount of morphological resemblance, especially in the involucres, flowers, and fruits, even though they are very distinct in habit, leaves, and pappus, as well as in the pubescence on the corolla tube, which again is intermediate in *C. Reuteriana*. The close relationship of *C. Reuteriana* to the other species in this section is obvious (cf. Part II, p. 649 and figs. 199-201).

Hostia, section 20, is certainly related to *Paleya*, section 7, although all nine species of *Hostia* are annuals. This relationship is shown by the peculiar outer involucral bracts in all three species of *Paleya* and in *C. alpina* and *C. syriaca*, the two most primitive species of *Hostia*; it is also shown by similarities in the leaves and especially in the achenes. These are long-attenuate in *C. albida* and beaked in the other two species of *Paleya*, whereas at least the inner ones are more finely beaked in all the species of *Hostia*. *C. albida* has $n=5$ chromosomes, as have all the species of *Hostia* except *C. Kotschyana*, a derived species; the karyotypes of six 5-paired species of *Hostia* and the karyotype of *C. albida* are also similar.

Pterotheca, section 22, with its one species, *C. sancta*, is karyotypically very similar to section 21 of Group I; but on morphological grounds it is much closer to *Lago-seris* (sec. 16, Group II), concerning which nothing is known cytologically. These morphological resemblances in habit, leaves, involucres, flowers, fruits, and the receptacular paleae extend in some parts to numerous fine details. Here, then, is the most obvious relationship of *C. sancta*; and its geographic distribution fits perfectly with the conception that this aggressive, widespread annual was derived from one of the endemic perennials in section 16 or a similar but now-extinct species. This is indicated by the dotted line connecting 22 and 16 in figure 4. It should be noted, however, that not only does considerable morphological resemblance exist between *C. sancta* and *C. multicaulis* of section 21 but that the karyotypes of the two species are very similar. On this basis it might appear that section 21 was also derived from section 16. But the other three species of section 21 show closer resemblance to section 5 than to section 16, so that the derivation of section 21 from the 1-5 line seems more probable (see fig. 4).

Zacintha, section 23, like section 14, has one primitive species and one very advanced species, the other two being intermediate. The first, *Crepis patula*, an Algerian endemic, is definitely primitive in the woody, modified-rhizome type of root, in the lyrate basal leaves, in the few medium-large heads, in the large florets, and in the large, many-ribbed achenes. In these respects it resembles *C. Strausii* and *C. Raulini* of section 10 more than any other species. This resemblance, however, is not particularly close, and it is probable that the immediate ancestor of *C. patula* is now extinct. As in *C. Reuteriana*, the peculiar root of *C. patula* certainly indicates a connection with the primary *Crepis* line. This species is remarkable in that, along with its primitive characteristics, it has become highly specialized in one respect and extremely reduced in another. The specialization referred to, that of the tendency of the involucre to remain closed in fruiting heads and to become indurate and, in the advanced species, more or less thickened, is also characteristic of the section as a whole. This tendency is extremely marked in *C. patula* (hence the name given by Poiret to the genus founded on it). In the most advanced member of the group, *C. Zacintha*, this tendency also holds, as it does in *C. Dioscoridis*, but to a less extent, and in *C. multiflora*, to a still less extent. The reduction in *C. patula* (mentioned above) is in the extremely short pappus, it being less than 0.5 mm long. In this peculiarity *C. patula* is unique, not only to the section alone, but in the whole genus. The smaller size of the 4 chromosomes of *C. patula*, as compared with those of *C. Dioscoridis* and *C. multiflora*, also suggests that, although this is a fairly

primitive species morphologically, yet it has actually undergone a number of reduction processes. Much greater reduction and specialization, however, is found in the 3-paired *C. Zacintha* which also has a fairly short pappus, only 1.5 mm long. This is a widespread annual of the Mediterranean region. *C. Dioscoridis* is indigenous in Greece, and *C. multiflora*, in the Aegean region. The significance of these distributions in relation to that of *C. patula* is worthy of consideration (see Part II, p. 742).

Phytodesia, section 24, contains ten species, the most primitive being the usually biennial species, *C. nicaeensis*. This species exhibits so many resemblances to *C. biennis* of section 10 that the two are often misidentified. Yet *C. nicaeensis* is definitely more reduced in the small outer involucral bracts, smaller florets, and smaller, 10-ribbed achenes. At the same time, the resemblance between the two is so marked as to warrant the assumption that the 4-paired *C. nicaeensis* was derived from a 5-paired ancestor of *C. biennis*, a polyploid species. Also, the similarities are sufficient throughout all ten species to support the derivation of this section from section 10, since they are all species of the Mediterranean region in the widest sense.

Lepidoseris, section 25, contains thirteen species, most of which are known to have $n = 4$ chromosomes, and all are of the Mediterranean region, including the Madeira and Canary archipelagoes and the Caspian region. The more primitive species, like *C. spathulata* and *C. canariensis*, with their strong perennial root, large leaves, leafy stem, and very shortly beaked achenes, show some resemblance to the primitive members of section 10; and it is not unreasonable to assume that they were derived from those or similar species. Although some of the species in the preceding section have shortly beaked achenes, this appears to be a parallel development in a similar but different line also derived from section 10. At the same time, it should be noted that some of the north African members of section 25 exhibit more or less resemblance to members of section 8. This is especially notable in the little-known *C. Claryi* of the Sahara Atlas in southern Algeria. In its habit, leaf shape, involucres, flowers, and fruits, this species shows more or less resemblance to *C. congoensis* or *C. ugandensis*. There is also marked similarity between the karyotype in section 25 and the karyotype of several species in section 8. There is nothing surprising in this, since both sections 8 and 10 are believed to have descended from species such as those now existing in section 6. This possibility that section 25 originated partly from section 10 and partly from section 8 or from common ancestors is indicated in figure 4.

Nemauchenes, section 26, consists of seven species, all of which are highly specialized, short-lived annuals, occurring mostly in Mediterranean littoral regions. Like the species of section 25, these plants show sufficient resemblance in habit, leaves, flowers, and fruits to species of section 10 to warrant the assumption that they were derived from them or from common ancestors. The section as a whole is characterized by peculiar modified marginal achenes; and those of *C. aspera* are sufficiently similar to those of *C. Dioscoridis* of section 23 to have caused de Candolle to place these species together in the genus *Endoptera*; but the two are so different in most respects that such a grouping is not at all justified. The similarity of the marginal achenes of *C. Dioscoridis* to those of *C. aspera* must represent parallel evolution.

Psammoseris, section 27, like many other sections of *Crepis*, contains perennial and annual species. But the four perennial species are all greatly reduced, especially the involucres and fruits; and the three annual species, all of which occur on the north African littoral, are the most extremely reduced and specialized species in the genus. Two of the perennials, *C. Rueppellii* of northeastern Africa, and *C. Forskalii* of an adjacent region in Arabia, are very similar and quite distinct

from the other perennials of this section. In gross morphology they are sufficiently like the more primitive species of section 25 to suggest that they also were derived from section 10 or from common ancestors. The other two perennials, *C. bellidifolia* and *C. bursifolia*, both of the north Mediterranean littoral, are very distinct from each other. *C. bellidifolia* is the more primitive of these two, and it is noteworthy that it also shows some resemblance to *C. leontodontoides* of section 9. This is the reason for the dotted line connecting these two sections in figure 4. It is difficult to say more about the three annual species than that they may have developed from members of section 10 or section 25 or similar now-extinct species.

SUMMARY

1) The Crepidinae is one of the eight subtribes of the tribe Cichorieae of the Compositae. In the Crepidinae, five phyletic lines, streams, or branches are recognized as having been derived from the primitive genus *Dubyaea*. One of these branches is the genus *Crepis*, and the one most similar to *Crepis* is the *Youngia-Ixeris* line, which must have had an Asiatic origin. But the *Hieracium-Tolpis* line may be considered just as closely related to *Crepis*. Furthermore, the most primitive species of *Hieracium* now exist in Europe, which might seem to indicate a European center of origin for this mesh. Nevertheless, the present author believes that the whole subtribe Crepidinae had its origin in Asia.

2) The twenty-seven sections of *Crepis* fall naturally into three groups: I, the rhizomatous species; II, the more primitive taprooted species; and III, the more advanced taprooted species.

3) Evidence has been presented showing that, in sections 6, 9, 11, 14, 16, 19, and 23, taprooted species have developed from rhizomatous ancestors. This evidence supports the assumption that all the taprooted species of *Crepis* developed from rhizomatous ancestors.

4) On the basis of this and other morphological evidence, together with evidence from interspecific hybrids and comparative karyology, it is assumed that sections 6–10, 20, and 23–27 represent a single phylogenetic line, with some cross connections; also that twenty-four of the twenty-seven sections represent a common stream of development from *Dubyaea*-like ancestors, along with many complex interrelationships.

5) The other three sections are also assumed to have arisen from the same *Dubyaea* ancestors as the rest of the genus. Section 17 (*C. napifera*) is an anomalous species the closest affinity of which appears to be with *Crepis*. Except for this species and the twelve species in sections 12 and 18, which are assumed to have originated through hybridization between *Crepis* or *Crepis*-like *Dubyaea* species and primitive *Ixeris*-like or *Youngia*-like *Dubyaea* species, the genus as a whole must be considered as monophyletic.

CHAPTER 5

THE GEOGRAPHIC DISTRIBUTION OF CREPIS

THE REGIONAL DISTRIBUTION OF CREPIS SPECIES

THE GEOGRAPHIC DISTRIBUTION of the individual species is discussed in connection with the interrelations of the species within each section in the taxonomic part of the monograph, and distributional maps are provided for most of the sections. The present discussion deals with the general aspects of distribution within the genus and of the genus as a whole in comparison with the distributions of related genera, the main purpose of this being to determine, if possible, the region of origin and early development of the genus. That a single center of origin for *Crepis* is to be assumed is certainly warranted by the morphological, cytological, and genetical evidence reviewed in preceding chapters. This evidence led to the definite conclusion that the genus is monophyletic. At the same time, the phylogenetic relations within the genus are very complex, and a careful study of geographic distribution should throw further light on these relations as well as on those between this genus and nearly related genera. Since the species have been arranged in three main phylogenetic groups, primitive, intermediate, and advanced, it will be of special interest to ascertain whether there is evidence of agreement with the general principle of Matthew (1915, p. 180) that at any one time in a large group of organisms showing close phylogenetic relations the most conservative will be found farthest from the center of origin and the most advanced, nearest to the center of origin. The data on distribution of the species are summarized by sections for each of the three large groups of sections in tables 5, 6, and 7.

Group I (table 5) includes the 30 rhizomatous species, of which 14 have a European distribution and 12 an Asiatic distribution; the other 4 occur in Asia Minor, the Caucasus region, and western Persia. The last area, being intermediate between most of Europe and most of Asia, could have received that part of its present flora which is not autochthonous from either continent; and it is well known that extensive migration occurred from both Asia and Europe into this region. Accordingly, in seeking an indication of the probable region of origin of *Crepis* on the basis of the present concentration of species, the intermediate region between Europe and Asia will not be considered as significant. Since in group I the number of species in Europe and Asia are equal, no inference can be drawn, on the basis of numbers alone, whether one or the other continent was the more probable region of origin of *Crepis*. When, however, we consider the relative primitiveness of the species, we find the European group to be on the whole the more primitive. This group includes *C. geracioides*, *C. viscidula*, *C. paludosa*, *C. pygmaea*, *C. lapsanoides*, *C. mollis*, *C. terglouensis*, *C. rhaetica*, *C. Jacquinii* (all with $n=6$), and *C. aurea* ($n=5$); whereas the Asiatic group includes *C. kashmirica* and *C. lyrata* ($n=6$), *C. sibirica* ($n=5$) and *C. hokkaidensis*, *C. chrysanthia*, *C. gymnopus*, and *C. praemorsa* (all with $n=4$), as well as the tetraploid *C. polytricha* ($x=4$); also included are *C. tibetica*, *C. Gmelini*, and *C. elongata*, which are all more primitive than either *C. multicaulis* of Asia or *C. incarnata* of Europe. The chromosome numbers of *C. tibetica*, *C. elongata*, and *C. Gmelini* are not known, but they are probably either 5 or 6. Thus, the chromosome numbers show that the European group has more of the primitive species, a fact in agreement with the morphological evidence. On chromosome numbers and relative primitiveness of the species, the evidence from group I seems to favor Europe slightly as the probable region of origin.

TABLE 5

DISTRIBUTION OF THE RHIZOMATOUS SPECIES OF CREPIS (GROUP I)
(Italicized names, being merely indicators of limits of distribution, are not counted in the species totals.)
(The number following each species is the haploid chromosome number.)

Section	Europe, north and middle: Mountains and plains	European Alps, including Pyrenees	Balkan Peninsula and Crete: Mountains	Asia Minor, Caucasus, W. Persia: Mountains	Eurasia, northern: Plains and mountains	Asia, Central and east: Mountains
1	<i>sibirica</i>		<i>geracioides</i> 6 <i>viscidula</i> 6		<i>sibirica</i> 5 — — — — — <i>paludosa</i> 6	— — — — — →
2						
3		<i>pygmaea</i> 6				<i>kashmirica</i> 6
4		<i>terglouensis</i> 6 <i>rhaetica</i> <i>Jacquini</i> 6	<i>aurea</i> 5 — — — — — →	<i>albiflora</i> 4 <i>dioritica</i> →	<i>hokkaidensis</i> 4 <i>chrysanthra</i> 4 <i>polytricha</i> 8	
5	<i>mollis</i> 6	<i>lapsanoides</i> 6	<i>smyrnaea</i> 6 <i>montana</i> 6 <i>Mungieri</i> 6	<i>willemetioides</i> 6 <i>hierosolymitana</i> 6	<i>lyrata</i> 6	
13			→		<i>gymnopus</i> 4 →	
21			<i>incarnata</i> 4		<i>praemorsa</i> 4 →	
No. of species	1	5	7	4	4	9

Totals: Europe, including western Eurasia (*C. paludosa*) 14 — 47 per cent.
Asia Minor, Caucasus, western Persia 4 — 13 per cent.
Asia, including eastern Eurasia (*C. sibirica*) 12 — 40 per cent.
30 — 100 per cent.

This evidence, however, must be considered along with the evidence from groups II and III; and, what is more important, the distribution of *Crepis* must be viewed in relation to that of the nearest related genera before attempting to formulate the most acceptable hypothesis. Furthermore, after this hypothesis has been set up, it must be reconsidered in the light of what is known concerning the origin and migration of floras in Europe and Asia.

Group II (table 6) includes the 109 more primitive taprooted species, of which 28 (26 per cent) occur in Europe and northwestern Africa, whereas 35 (32 per cent) occur in Asia and North America. It will be noted again that the species of Asia Minor, Caucasus, and western Persia are not taken into account in comparing concentrations in Europe and Asia, since they could have come from either region. For the same reason the species of the Mediterranean littoral and of tropical and south Africa are also ignored at this time; although, as is shown elsewhere (see p. 109), the probability is actually better that these African species migrated from Asia rather than from Europe. Of the 28 European and northwest African species (table 6), 7 have $n = 5$ and 14 have $n = 4$ chromosomes, 1 polyploid has $x = 5$, and of the 6 remaining, which have not been studied cytologically, none is likely to have more than 5 pairs and most of them probably have 4. Of the 35 Asiatic and North American species, 3 have $n = 7$, 3 have $n = 4$, 1 tetraploid has $x \times 4$, 10 polyploids have $x = 11$, and 18 have not been studied cytologically. Of these 18, 4 in section 12 very probably have $n = 7$, and all the others probably have either 5 or 4 pairs. On the basis of chromosome numbers in group II, the Asiatic species are definitely more primitive than the European species. But morphologically they are almost evenly balanced, the primitive species of Europe, *C. pontana* and *C. blattarioides* (sec. 6) and *C. albida* (sec. 7), being offset by *C. subscaposa*, *C. darvasica*, *C. songorica*, *C. turcomanica*, *C. khorassanica*, *C. oreades*, *C. ircutensis*, and *C. Bungei* of Asia, together with the 8 fairly primitive species of sections 16, 17, and 18, which have none comparable to them in Europe. From group II, therefore, the evidence on chromosome numbers and relative primitiveness of the species favors Asia as the region of origin to about the same degree that the evidence from group I favors Europe.

Comparable evidence from group III (table 7) can hardly be considered as significant as that from groups I and II because most of the species are advanced and, regardless of their present location, may have been derived from either Asia or Europe. Of the 18 species in Europe and northwest Africa, 17 are advanced species, 14 of these being in sections 23–27. Only *C. patula* can be considered as fairly primitive. Of the 6 species in Asia and adjacent northeast Africa, 4 are in section 20 and 2 in section 27.

On the basis of numbers of species alone, the distribution for the entire genus may be summarized as follows:

	Number of species	Per cent of total
Europe and northwestern Africa.....	59	30
Asia and North America.....	54	28
Asia Minor, Caucasus, western Persia.....	34	17
Africa, tropical and south.....	28	14
Mediterranean littoral and Canary and Madeira Islands.....	21	11
	196	100

The numbers in Europe and in Asia and North America combined can hardly be considered as significantly different. Added to this is the fact that Europe as a whole has been thoroughly botanized, whereas the mountains of Asia as a whole

TABLE 6

DISTRIBUTION OF THE MORE PRIMITIVE TAPROOTED SPECIES OF CREPIS (GROUP II)

(Italicized names, being merely indicators of limits of distribution, are not counted in the species totals. The number following each species is the haploid chromosome number.)

Section	European Alps (secs. 6 and 8): Lower altitudes (sec. 10)	Spain-Italy, Morocco: Montane	Balkan Peninsula, including Crete: Montane	Asia Minor, Syria, Palestine: Montane
6	<i>pontana</i> 5 <i>conyzaefolia</i> 4 <i>blattaricoides</i> 4		<i>conyzaefolia</i>	<i>conyzaefolia</i>
7		<i>albida</i> 5		
8	<i>alpestris</i> 4			<i>alpestris</i>
9		<i>tingitana</i> 5 <i>leontodontoides</i> 5		
10	<i>biennis</i> <i>pannonica</i>	<i>latialis</i> 4 <i>chondrilloides</i> 4 --- <i>Triasii</i> 4 <i>oporinoides</i> 4	<i>bertiscea</i> --- → <i>Baldaccii</i> 5 <i>auriculaefolia</i> <i>biennis</i> 20 10 others 5, 4	<i>bupleurifolia</i> <i>macropus</i>
11		<i>Hookeriana</i> 4 <i>Faureliana</i>	<i>Schachtii</i> 5 ← -----	<i>pinnatifida</i> <i>bithynica</i> 5 <i>Robertioides</i> 4
12				
14				
15				
16				<i>frigida</i>
17				
18				
No. of species	4	9	15	6

Totals: Europe and northwestern Africa (4 + 9 + 15)	28	—	26 per cent.
Asia Minor, Caucasus, western Persia	17	—	15 per cent.
Asia and North America (24 + 11)	35	—	32 per cent.
Africa, tropical and south	28	—	26 per cent.
Mediterranean littoral	1	—	1 per cent.
	109	—	100 per cent.

TABLE 6

(Continued from facing page.)

(For totals of numbers of species arranged in accordance with areas of distribution, see bottom of table on facing page.)

Caucasus region and W. Persia: Montane	Asia, from E. Persia and Turkestan eastward: Montane	Africa, tropical and south: Montane (mostly)	Mediterranean littoral	North America: Montane (mostly)
<i>conyzaefolia</i>	<i>conyzaefolia</i>			
<i>elymaitica</i>		<i>achyrophoroides</i>		
	<i>subscaposa</i>	24 species, six have 4		
			<i>suberostris</i> 5	
Strausii sonchifolia ciliata 20 dens-leonis pannonica 4	<i>darvasica</i> <i>songorica</i> <i>khorassanica</i> <i>turcomanica</i> <i>pannonica</i>			
armena heterotricha demavendi	<i>oreades</i> 4 <i>crocea</i> 8	<i>tenerima</i> <i>xylorrhiza</i> <i>abyssinica</i>		
	<i>nana</i> 7 <i>flexuosa</i> 7 4 others			<i>nana</i> <i>elegans</i> 7
	<i>ircutensis</i> <i>Bungei</i> 4 <i>tectorum</i> 4			
				<i>monticola</i> 11 9 others 11
sahendi purpurea	<i>connexa</i> <i>elbrusensis</i>			
	<i>napifera</i>			
	<i>Phoenix</i> 4 others			
11	24	28	1	11

TABLE 7

DISTRIBUTION OF THE MORE ADVANCED TAPROOTED SPECIES OF *CREPIS* (GROUP III)
 (Italicized names, being merely indicators of limits of distribution, are not counted in the species totals. The number following each species is the haploid chromosome number.)

Section	Europe: Lower altitudes	Spain-Italy, Algeria- Tripolitania: Montane (mostly)	Balkan Peninsula, including Crete: Lower altitudes	Asia Minor, Syria-Palestine: Lower altitudes
19			Stojanovi 4	Reuteriana 4 4 other spp. 4
20	<i>foetida</i>		rubra 5 tybakiensis	<i>alpina</i> <i>syriaca</i> 5 <i>foetida</i> 5
22	<i>sancta</i>			<i>sancta</i> 5
23		patula 4	Dioscoridis 4 Zacintha 3	multiflora 4
24	capillaris 3	<i>nicaeensis</i>	<i>nicaeensis</i> 4 <i>neglecta</i> 4 <i>fuliginosa</i> 3 2 other spp. 4	insignis
25		Claryi	vesicaria 4	
26	<i>setosa</i>	amplexifolia 4	setosa 4	<i>aspera</i> 4
27		bellidifolia 4 bursifolia 4		
No. of species	1	5	12	11

Totals: Europe and northwestern Africa	18	—	32 per cent.
Asia Minor and Caucasus region	13	—	23 per cent.
Asia and adjacent northeastern Africa	6	—	10 per cent.
Mediterranean littoral and oceanic islands	20	—	35 per cent.
	57	—	100 per cent.

TABLE 7

(Continued from facing page.)

(For totals of numbers of species arranged in accordance with areas of distribution, see bottom of table on facing page.)

Caucasus region: Lower altitudes	Asia, from Persia and Turkestan eastward: Lower altitudes	Africa, northeastern and S. Arabia: Montane	Mediterranean littoral	Madeira and Canary Islands
<i>alpina</i> 5 ----- →	<i>Thomsonii</i> 5	<i>Schimperi</i> <i>eritreensis</i> 5		
<i>foetida</i>	<i>Kotschyana</i> 4			
----- →				
	<i>parviflora</i>		<i>parviflora</i> 4 <i>apula</i> 4 <i>Suffreniana</i> 4	
<i>Marschallii</i> 4			<i>spathulata</i> <i>Salzmannii</i> <i>Clausonis</i> 4 4 other spp. 4	<i>canariensis</i> 4 <i>divaricata</i> 4 <i>Noronhaea</i> 4 <i>vesicaria</i>
→			<i>juvenalis</i> 4 <i>aculeata</i> 4 2 other spp. 4	
		<i>Rueppellii</i> <i>Forskallii</i>	<i>nigricans</i> 4 <i>filiformis</i> <i>senecioides</i> 4	
2	2	4	17	3

have been comparatively little explored. It is safe to predict that numerous species of *Crepis* remain to be discovered in Asia as well as in Africa. In Asia, especially, it is not improbable that some of these undiscovered species are among the more primitive in the genus. But on the basis of existing evidence on numbers of species now occurring in Europe and Asia, it is impossible to draw any conclusion concerning which continent was probably the region of origin of the genus. However, the evidence on the distribution of closely related genera and on the distribution of species in the primitive sections of *Crepis* leads to a definite hypothesis.

THE DISTRIBUTION OF RELATED GENERA

In the subtribe Crepidinae, as defined by Stebbins (cf. p. 62), the larger or more critical genera, other than *Crepis*, and their present distributions are as follows:

1) *Dubyaea*, from which all the genera in the subtribe are assumed to have originated, and its close derivative, *Soroseris*, are restricted to the Sino-Himalayan region. That this was not their actual place of origin, or that of the Crepidinae, but rather that they probably moved in here from the Altai-Tien Shan region will be developed in the following chapter.

2) *Youngia* and *Ixeris*, the closest relatives of *Crepis*, are distributed in southeastern Asia, for the most part between the seacoast and the Pamir and Altai mountains, with *Youngia* extending more to the west and *Ixeris* more to the east and south (cf. Babcock and Stebbins, 1938). *Chondrilla* occurs in China and Siberia, but has become distributed as far west as Europe. *Taraxacum* has some of its most primitive species in southern Europe, some in Asia Minor, and many others in Central Asia. Handel-Mazzetti (1907) reached the final conclusion that this world-wide genus had its "cradle" in the "heart of Asia" and that this generalization agrees with others repeatedly obtained in analogous investigations. Such a definite conclusion by such an eminent authority, concerning a closely related genus with a comparable distribution, must be recognized as having an important bearing on the present problem.

3) *Prenanthes* has its present center of distribution in eastern Asia and extends into North America, Europe, and tropical Africa. In this connection it is of special interest, as was pointed out by Stebbins (1937b), that *P. subpeltata*, the only species of *Prenanthes* known from the African continent, "has its closest relatives in the temperate rain forests of the Sino-Himalayan region at corresponding altitudes." *Lactuca*, which is considered by Stebbins to be essentially monophyletic and yet "broad-based," i.e., derived from a group of rather diverse but interrelated species, has three main centers of distribution. One of these is southeastern Asia, another is Asia Minor and southeastern Europe, and the third is southwestern tropical Africa (Belgian Congo and Angola). The distribution of neither of these genera is adverse to the idea of an Asiatic origin; in fact, a Central Asiatic center is strongly indicated for both of them.

4) *Launaea* and *Sonchus*. The connection between these genera and *Dubyaea*, according to Stebbins, is obscure, but yet they certainly belong to this subtribe. The most primitive species are in northwestern Africa (Atlas Mountains), Spain, and the Madeira and Canary Islands. These genera are related to *Tolpis*, which is strictly European and north African. Hence, there is no clear evidence that either of these genera originated in Asia.

5) *Hieracium* is the most widespread of all the genera of the Crepidinae, but its most primitive species as well as the greatest range of variability and the strongest development of the genus are in central and northern Europe. *Tolpis* and some

other small genera close to *Hieracium* are primarily western Mediterranean genera, and, like *Launaea* and *Sonchus*, their most primitive species occur in Madeira and the Canary Islands.

From the foregoing review it appears that the general picture of geographic distribution in the Crepidinae suggests an Asiatic origin for *Dubyaea*, *Soroseris*, *Youngia*, *Ixeris*, *Taraxacum*, *Chondrilla*, *Prenanthes*, and *Lactuca*. Only in the *Hieracium-Tolpis* and the *Launaea-Sonchus* lines is the present distribution predominantly European. In *Launaea*, *Sonchus*, and *Tolpis*, the distribution of their most primitive species in the western Mediterranean region is strictly comparable to the occurrence in Spain and Italy of some of the most primitive species of *Taraxacum* and *Crepis*. It is only necessary to assume that the connection between those small western Mediterranean genera and *Dubyaea* is obscure because their more *Dubyaea*-like ancestors which lived farther to the east are now extinct. Considering its world-wide distribution, it would appear at first glance that a similar assumption might be made for *Hieracium*. But I am informed by Stebbins (oral communication) that all of the Asiatic species of subg. *Euhieracium* are apomictic. Furthermore, the American subgenera, *Stenotheca* and *Mandonia*, are specialized, derived groups. This evidence, together with the occurrence of the most primitive species in Europe, seems to favor a western Eurasian rather than a Central Asiatic origin for this genus. Nevertheless, *Hieracium*, like *Launaea*, *Sonchus*, and *Tolpis*, must be assumed to have originated from *Dubyaea* or *Dubyaea*-like ancestors.

In this connection, mention should be made of an alternative hypothesis concerning the possible region of origin and early migration of the ancestral stocks that produced the Asiatic and European lines of the Crepidinae. It is possible that the *Dubyaea*-like ancestors of these two groups of genera developed as a branch of the pre-Tertiary arctic flora in the region of the northern Ural Mountains. Then, in early Eocene time, before the Obic Sea separated Europe from Asia, certain *Dubyaea*-like plants which later gave rise to the *Hieracium-Tolpis* and *Launaea-Sonchus* lines migrated into northern Europe, where they continued to develop throughout the Tertiary period until they were driven southward or were exterminated by increasing cold; whereas the ancestors of *Dubyaea*, *Soroseris*, and the *Prenanthes-Lactuca*, *Youngia-Ixeris*, and *Crepis* lines migrated into north Central Asia and became established in the Altai-Tien Shan region. This assumed scheme is consistent with the facts concerning the present preponderance in Europe and the Mediterranean region of *Hieracium*, *Tolpis*, *Launaea*, and *Sonchus*, and with a Central Asiatic origin for the other larger genera of this subtribe. But this hypothesis assumes the differentiation of the *Dubyaea*-like ancestors of the Crepidinae into distinct *Hieracium*-like and *Crepis*-like forms by early Eocene, something which is difficult to imagine in the light of the history of the Angiosperms as a whole. The very earliest seed plants appeared only in the preceding period (Seward, 1941, p. 383). Furthermore, this scheme does not harmonize with the location and history of the Ural and the Altai in relation to Angara, which is, it seems, the most probable region of origin of the Angiosperms (see p. 93). The Altai has been a part of Angara Land since the Carboniferous period (see p. 95), whereas the Ural was completely cut off from this region by the Obic Sea from mid-Eocene to mid-Oligocene (see figs. 5 and 6). It seems more probable, therefore, that the whole subtribe Crepidinae had its origin in Angara and particularly in the Altai.

THE DISTRIBUTION AND CENTER OF ORIGIN OF CREPIS SPECIES

The rhizomatous species.—The distribution of the species in the more primitive sections will now be examined with reference to the possible origin of *Crepis* in Central Asia, with the understanding that the western Altai and Tien Shan mountains are included in the area. Among the rhizomatous species, sections 1, 3, and 5 will first be examined, then sections 2 and 4. In section 1, *C. geracioides* and *C. viscidula* occur in the Balkan Peninsula, the former being lower montane in association and the latter subalpine or alpine. *C. geracioides* is definitely a southern species; and, since *C. viscidula* occurs only in Bulgaria and *C. geracioides* is its closest relative, it is also southern in its affinity. *C. sibirica* is a diminishing relic in the Carpathian region, is common in Russia and northern Asia from the Urals to Transbaikalia, and occurs in the mountains of western Mongolia and eastern Russian Turkestan. It is listed by Pax (1898, p. 226) as one of six flowering plants comprising a typical "Siberian" element in the flora of the Carpathian Mountains. *C. paludosa* extends throughout most of middle and northern Europe and into western Siberia. This species presents a special problem because of its intermediate character between *Crepis* and *Hieracium*. If it actually originated through hybridization between primitive members of those genera, as seems probable, the event could have occurred during a common migration into northern Europe through the Turgai region south of the Ural Mountains. The geological and vegetational history on which this statement is based is reviewed in chapter 6. At any rate, *C. sibirica* and *C. paludosa* probably migrated from Central Asia into Europe by some such northern route, whereas *C. geracioides* and *C. viscidula* must have taken a southerly route. That a route to the south and west was followed by *C. pygmaea* of southern Spain and the southwestern Alps, and by seven of the eight species of section 5, is strongly indicated by the distribution of these seven species: one in Central Asia, one in northern Persia, one in Palestine, one in eastern Asia Minor and Greece, another in Greece, one in Crete, and one in the Pyrenees. *C. mollis*, the other member of section 5, is widely distributed in middle Europe, and it occurs mostly at low elevations. Its closest affinities are all southern. It is worthy of note that in this section, in which sufficient traces have been preserved, there is good conformity with Matthew's general principle. Only to the extent that *C. montana* of Greece and *C. Mungierii* of Crete are more reduced in size than *C. willemetoides* of Persia, is there incomplete conformity with this principle. Furthermore, *C. lapsanoides* of the Pyrenees is certainly the most primitive species of this section.

The primitive *C. kashmirica* (section 2), like *Dubyaea oligocephala* and *D. hispida*, probably moved into the western Himalaya region from farther north in the late Tertiary or early Quaternary period. *C. kashmirica* is an alpine species occurring at altitudes from 3,500 to 4,300 meters; hence it could not have occupied its present area until postglacial time. From its present conditions of life, it appears that it could not have survived if it had ever started to migrate southwestward from Central Asia along the route which was probably followed by the primitive *Crepis* species of southern Europe.

In section 4 the relationship to an assumed center in Central Asia is beyond doubt. In nine species—one in northern Japan, two in northern Asia (one from Altai to Transbaikalia, the other from Altai to Kamchatka and on the arctic Eurasian tundras), two in Asia Minor, another extending from Asia Minor through the Balkan countries to Italy and the Alps, and the three most primitive species endemic in the Alps—we find a distribution that could hardly indicate more clearly a center

of distribution in Central Asia. This section also conforms with Matthew's principle which is summarized on page 75.

The evidence from sections 13 and 21 also strongly indicates an Asiatic center of distribution. In the first group, *C. gymnopus*, which is the most primitive of the three species, is endemic in Japan; *C. praemorsa* extends from Manchuria through Siberia to the Altai and from the Urals across Russia and middle Europe as far as Scandinavia and northern Italy; *C. incarnata*, which was evidently derived from *C. praemorsa*, is restricted to a small area in northeast Italy, southeast Switzerland, southern Austria, and the western Balkan Peninsula. In the last section, *C. tibetica* and *C. elongata* occur in eastern Tibet, western Szechuan, and northern Yunnan, and *C. Gmelini* is in eastern Siberia. All three are definitely more primitive than the polymorphic *C. multicaulis*, which extends from the western Himalayas through the mountains of Turkestan to the Altai Mountains and occurs in a small district in northeastern Norway. This district, Varanger in Finmarken, is part of that narrow strip of northernmost Scandinavia which, according to both Hulten (1937) and the Great Soviet world atlas, Pt. I (1937, cf. Hobbs, W. H., Science 104 [2692] : 106. 1946), was not covered by Pleistocene ice. Evidently, this species, like *C. sibirica* and *C. paludosa*, migrated from Asia into northern Europe.

The more primitive taprooted species.—Turning next to the more primitive taprooted species we find in section 6 four species that differ rather strikingly from one another in distribution. *C. pontana*, the most primitive, occurs in the western European Alps and southeastward in the mountains of the western Balkan Peninsula at elevations from 1,200 to 2,500 meters. *C. blattarioides* occurs from 700 to 2,200 meters in elevation in the Pyrenees, throughout the Alps, and in the western Balkan Peninsula. These two species occur mostly on limey soils. The occurrence of these alpine and subalpine relics in southern Europe may at first appear to throw doubt on the probability of their origin in Asia, especially since they have been recognized by some European botanists as part of the autochthonous flora of the Alps (cf. Diels, 1910). It happens, however, that one other species in this section provides the stations by which the origin of this section can be traced back to Central Asia. *C. conyzaeifolia*, which is next in degree of primitiveness to *C. pontana*, occurs from the Pyrenees through the Alps to the Balkan Peninsula and Carpathian Mountains, also in northern Asia Minor, Transcaucasia, northern Persia, and the Altai Mountains. Although often mentioned as a subalpine or alpine species, it is known to occur between 600 and 3,000 meters, and its usual altitudinal range is from 1,000 to 2,000 meters. Furthermore, this species flourishes on soils deficient in lime, including schists; and it has been reported in sterile meadows on dry sod and in open swampy woods. Evidently, it is a much more adaptable species than the other three, and this probably accounts for its ability to persist in places along the route of migration from the assumed center of origin to its farthest outpost in the Pyrenees.

Section 7 includes three species with interesting distributional relations. *C. albida*, the most primitive one, is a polymorphic, lower montane species distributed mostly in Spain, with outlying stations in southern France, northwestern Italy, the Balearic Islands, and northern Morocco. The next most primitive species, *C. achyrophoroides*, is endemic in northern Abyssinia, and the most advanced species, *C. elymaitica*, is known from only two collections in the high mountains of western Persia. Even in this small group, on the assumption that the center of origin was in Central Asia, we again find excellent conformity with Matthew's principle.

Section 8 is the next in size to the largest section in the genus and, except for two species, *C. alpestris* and *C. subscaposa*, it is distributed entirely in tropical and south Africa. The first-mentioned is distributed in western Asia Minor, the western

Balkan states, the Apennines, the eastern Alps, and the western Carpathian Mountains. On the basis of the characters used for sectional delimitation, *C. alpestris* belongs in this group. At the same time it exhibits considerable morphological resemblance to *C. conyzæfolia*, the widespread member of section 6. Like *C. conyzæfolia*, too, it has a wide altitudinal range, 500 to 2,650 meters; but it usually occurs on limey soil which may have a bearing on its failure to occur farther eastward. At any rate, *C. alpestris* is actually a connecting species between the two sections and serves as a good indicator of the probable development of section 8 from the same center of origin as section 6. *C. subscaposa* of southwestern China, northwestern Burma, and western Indo-China is closely similar throughout to the species of the larger, more advanced subsection of section 8. So far as is known, it has no close relatives in Asia, its resemblance to the anomalous *C. napifera* being limited to the root, the caudical leaves, and the erect, nearly leafless stem, whereas the type of inflorescence, size of heads and number of florets, involucral characters, and surface of the receptacle, as well as the flowers and fruits, all resemble those of the African species. Hence, *C. subscaposa* and *C. napifera* must represent widely divergent lines which probably arose from the same ancestral stock. *C. subscaposa*, therefore, adds considerable weight to the evidence from *C. alpestris*, showing that the twenty-six species in section 8 all stem originally from a Central Asiatic source. *C. subscaposa* is one of the more advanced species in this section and *C. alpestris* one of the most primitive, but *C. kilimandscharica* and *C. keniensis* of the two highest mountains of northeastern tropical Africa are both more primitive than *C. alpestris*. Hence, in this section also we find general conformity with Matthew's principle.

The three species in section 9 all occupy areas in the western Mediterranean region, but the most primitive species, *C. tingitana* of Spain and Morocco, is farthest to the west. *C. leontodontoides* is intermediate, but, as was indicated by the results of hybridization experiments, is still fairly primitive. It is distributed in western Italy, Sardinia, Corsica, and southern France. *C. suberostris*, an advanced, annual species, occurs on the western Algerian littoral and adjacent upland. These geographical relations fit in well enough with the general picture of distribution in the genus with reference to an Asiatic origin.

In both sections 10 and 11 the range of distribution is just as consistent with an Asiatic origin as it is in the widely distributed sections already discussed (see table 6). The fact that some of the most primitive species in both sections occur in Turkestan and Persia, whereas others are found in the Caucasus and Balkan regions, is understandable on the basis that they, being actually less primitive groups than those discussed above, have had less time and opportunity to become dispersed sufficiently to conform closely with Matthew's principle. This principle, however, was found to apply well to the distribution of sections 3, 4, 5, 7, 8, and 9. Furthermore, section 6 is in general agreement with it; and we have seen that the restriction of section 2, *C. kashmirica*, to very high altitudes in the western Himalayas is sufficient in itself to explain the failure of this species to get farther from the assumed center of origin. On the other hand, the persistence of *C. sibirica* (sec. 1) in the exact region of the assumed center of origin is certainly an exception to Matthew's principle. But this is a widespread species; whereas *C. geracioides*, which is even more primitive in some respects, is a local endemic situated far from the assumed center.

The Asiatic sections, 12, 16, 17, and 18, together with the North American extension of section 12 and the wholly American section 15, are all in perfect agreement with the hypothesis that the genus originated and was dispersed from Central Asia.

The most advanced species.—Finally, the most advanced sections of *Crepis* are all distributed in the Mediterranean region, some of them extending as far east as northwestern India and Turkestan, and some occurring as far west as Madeira. This concentration of the most advanced sections in the general region of the Mediterranean Sea is wholly consistent with the hypothesis that the ancestors of these species came from Central Asia. The highest development of the genus in this region is a natural result of the topographic and climatic changes that have taken place there since Tertiary times.

CONCLUSION

This review of the geographic distribution of *Crepis* species and of the genera closest to *Crepis* leads very definitely to the conclusion that the center of origin and early development of *Crepis* was in Central Asia, probably in the Tien Shan-Altai region. Further consideration is given to this hypothesis from the standpoint of geology, paleobotany, and vegetational history in the following chapter.

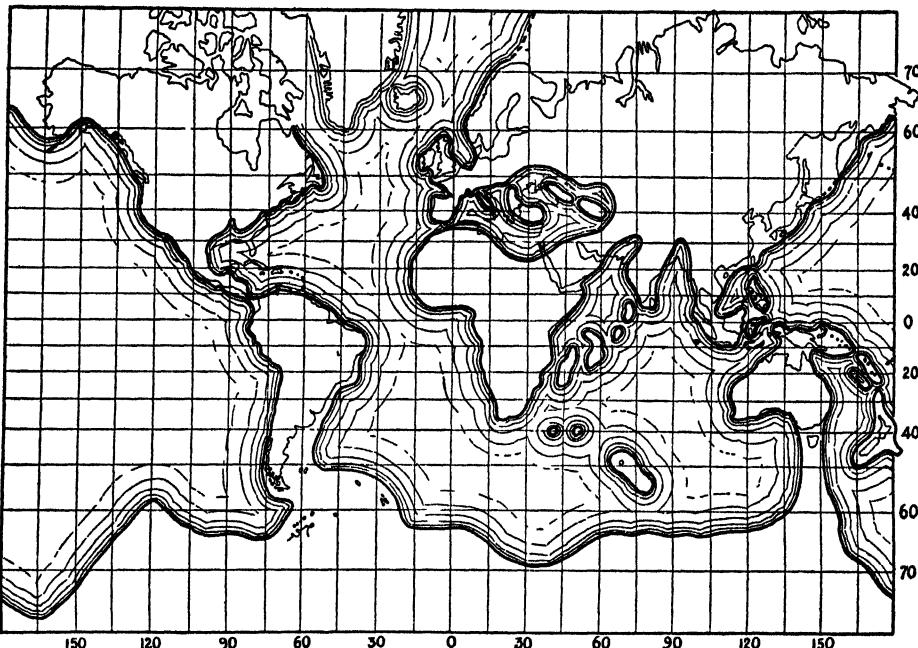
CHAPTER 6

ASIATIC-EUROPEAN PLANT MIGRATION AND ITS BEARING ON THE PRESENT DISTRIBUTION OF *CREPIS*

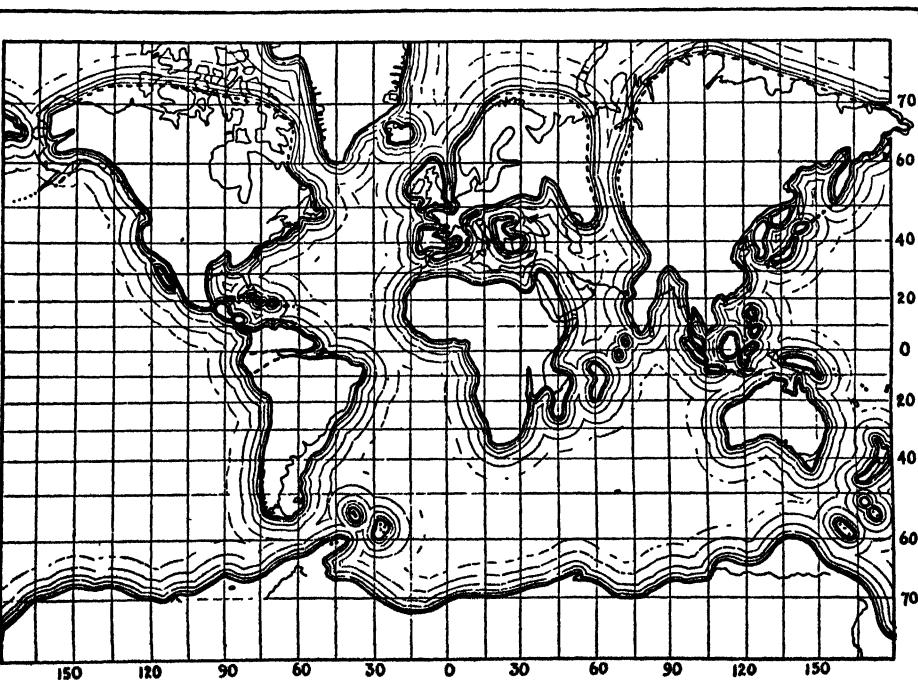
BEFORE PROCEEDING to describe the probable course of development of *Crepis*, it is necessary to examine the general background of floristic history in Eurasia since the Mesozoic era. In attempting to envision the general aspects of the development and migration of Eurasian flowering plants, the author has consulted numerous treatises on the distribution of extinct and living species. The Tertiary fossil record in Europe is rich and the literature correspondingly extensive. In addition to the well-known book of Seward (*Plant Life through the Ages*, 1941), there are fortunately a number of excellent general reviews of this literature as well as some fairly recent reports of investigations by competent authorities in this field. A very helpful general view of the geological history of Asia was found in *The Structure of Asia*, edited by J. W. Gregory (1929); and the works of Fickeler (1925) and of Berkey and Morris (1927) on the geology of Altai and Mongolia have provided valuable supplementary information. Matthew's standard works on Tertiary continental outlines and climate and evolution have, of course, been invaluable aids. In addition to these books, numerous papers have been consulted. In basing assumptions on the evidence in some of these papers, it is realized that there is a certain element of risk in relying on the identification of fossil plant materials. For this reason, in questions of critical importance I have tried to use evidence from paleobotanists of widely recognized standing, although this has not always been possible. With the help of this literature I have attempted in this chapter to give, in as brief form as possible consistent with clarity, a general picture of earth history in Eurasia since the Mesozoic era, with special reference to the development and migration of the flowering plants, particularly of *Crepis*. Since completing Part I of this monograph, Wulff's excellent work, *An Introduction to Historical Plant Geography* (1943), has come to hand. It is reassuring to find that the principles and methods adopted by the present author are in close agreement with those advocated by Wulff, especially in connection with the location of centers of origin and the migrations of species. The theory of continental drift (Wegener, 1924) need not be considered in connection with the origin and migrations of *Crepis*, since this is essentially a northern group which must have migrated into Africa during the Tertiary period.

CONTINENTAL OUTLINES IN THE TERTIARY PERIOD

Geologists are in general agreement that important changes in the outlines of the continents occurred during the Tertiary period. These changes are clearly indicated on the six maps prepared by Matthew (1906) which are reproduced in figures 5-7. Carefully prepared from the best geographical, paleontological, and zoölogical data available at the time, it is probable that these maps are in the main fairly dependable; although, as Matthew states: "The European continent presents a very complicated problem and considerable parts of the outlines shown must be admitted to rest on pretty slender evidence." Thus, the relative widths of the seas separating Europe and Africa, as well as Europe and Asia during certain intervals, may be subject to some modifications; but the fact that such seas existed and their relative positions are much more pertinent to the present discussion than their

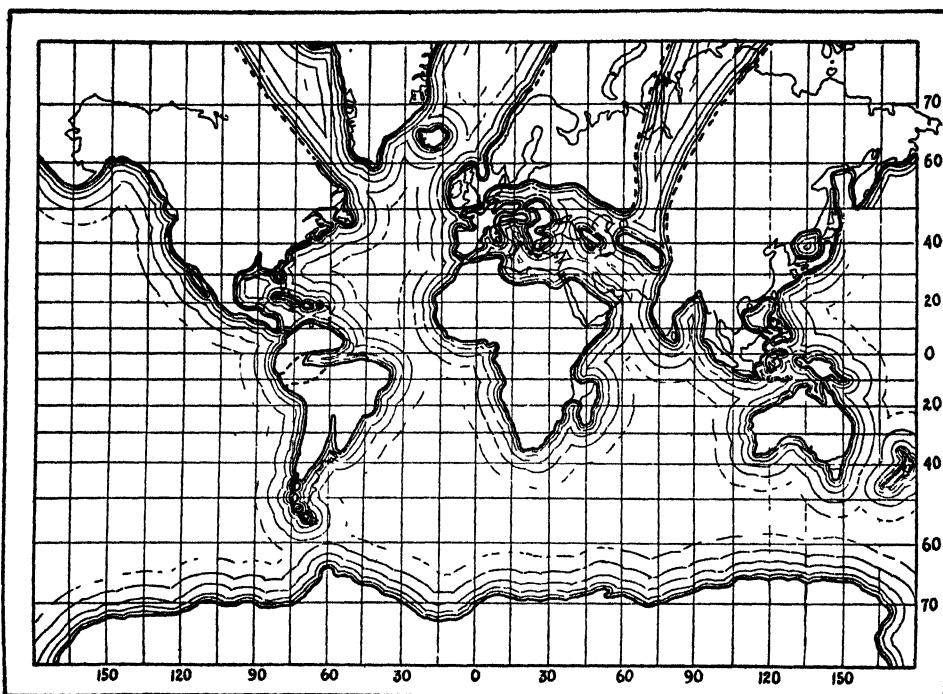


HYPOTHETICAL CONTINENTAL OUTLINES—POST-CRETACEOUS

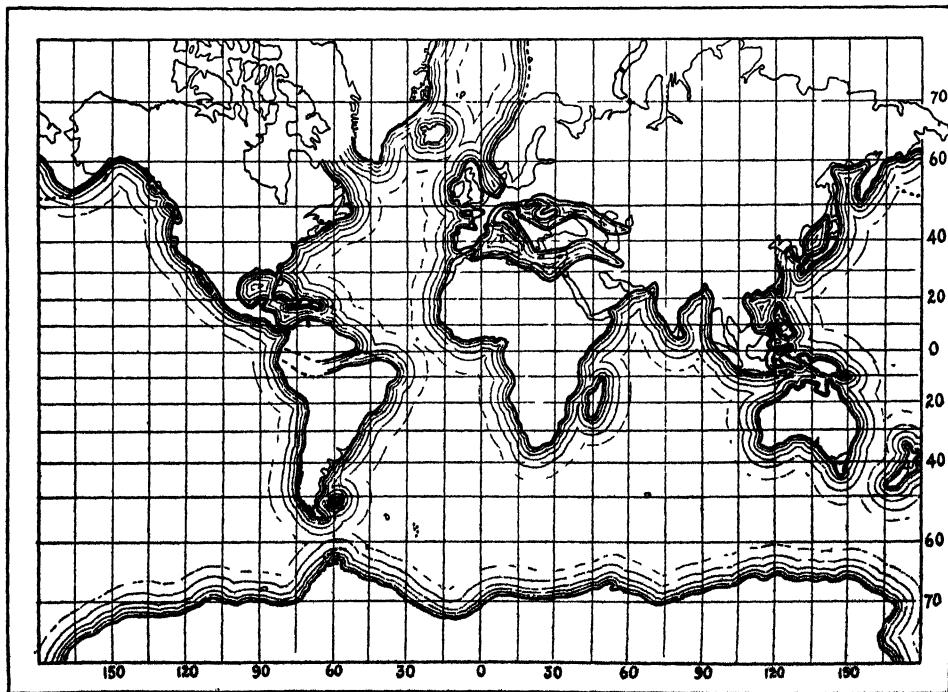


HYPOTHETICAL CONTINENTAL OUTLINES—MIDDLE EOCENE

Fig. 5. Maps 1 and 2 of Matthew's hypothetical continental outlines—post-Cretaceous (above) and Middle Eocene (below).

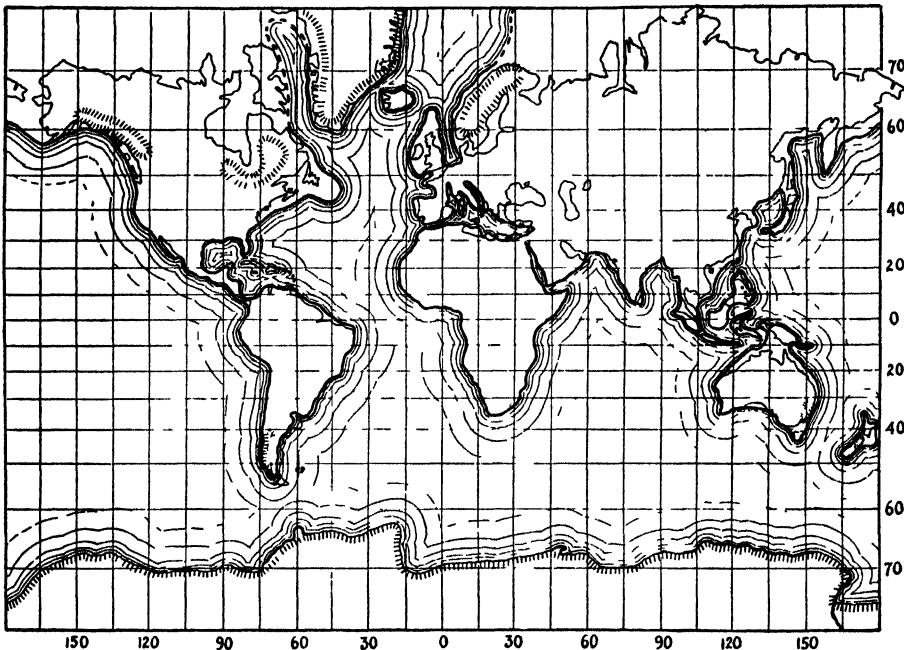


HYPOTHETICAL CONTINENTAL OUTLINES—MIDDLE OLIGOCENE

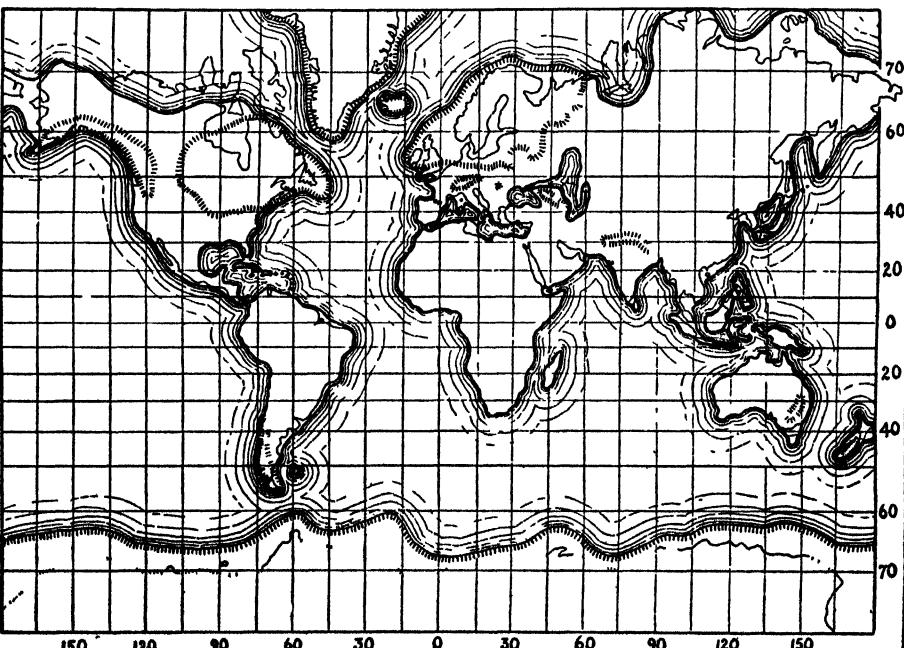


HYPOTHETICAL CONTINENTAL OUTLINES—MIOCENE

Fig. 6. Maps 3 and 4 of Matthew's hypothetical continental outlines—Middle Oligocene (above) and Miocene (below).



HYPOTHETICAL CONTINENTAL OUTLINES—PLIOCENE



HYPOTHETICAL CONTINENTAL OUTLINES—EARLY PLEISTOCENE

Fig. 7. Maps 5 and 6 of Matthew's hypothetical continental outlines—Pliocene (above) and early Pleistocene (below).

approximate sizes. The high lights of the six consecutive geological ages represented by the maps have been condensed from Matthew's description, with some added notes on floras based on Seward (1941). It is to be remembered, of course, that the whole process of earth history is continuous and the best that can be done in a brief series of descriptions is to note the points of most significance for the problem in hand.

Post-Cretaceous.—During and after Cretaceous there was a great extension of the sea over land areas, the continents were isolated and oceanic climate probably extended mild, moist conditions widely over the lands. It was the age of reptiles. At its end there was a great upheaval in both the Northern and Southern Hemispheres, with great intermigrations. Old faunas and floras vanished and mammals and flowering plants appeared.

Middle Eocene.—The sea again insulated the six great land masses. *Europe and Asia were separated east of the Ural region by the "Obic Sea."* Each continent then developed a peculiar fauna. That the climate was warm, moist, and equable is indicated by the record of plant fossils which reveal the existence of dense forests over large areas. Herbaceous plants were relatively few.

Middle Oligocene.—The continents had partly emerged and Asia and North America were connected by a broad area in the north. But South America, Africa, and Australia remained separate. Europe and Asia were still separated by the Obic Sea; but this barrier to plant migration was removed, at least in part by the end of Oligocene.

Miocene.—The continents had emerged further, somewhat reducing Tethys, the great central sea of Europe and Asia. But this now consisted of two great arms that reached eastward beyond the present Caspian Sea. *And it is worth noting* that the peninsula separating these two arms included part of Iran (Persia) and the Caspian region, the northern part of Asia Minor and part of the Balkan Peninsula, and northern Italy, thus making a complete land connection between Asia Minor and southern Europe. In the north *Asia and Europe were continuous*; and Asia was still connected with North America through "Beringia." This connection persisted until Pleistocene. *Africa was connected with Asia across Arabia*, thus permitting extensive intermigration of plants and animals. The latter part of this age probably brought the increase of cold climate at the poles, with its gradually increasing effects upon the general trends of plant migration in the Northern Hemisphere. North and South America were not yet completely connected.

Pliocene.—Elevation of all the continents continued generally, but Africa was again nearly cut off by the Red Sea. South America was united with North America. Tethys was reduced almost to the present size of the Mediterranean Sea. Probably the great elevation of northern Eurasia and northeastern America and the increasing polar cold initiated the glacial epoch in Greenland, Labrador, and Norway, with consequent increasing plant migration from north to south.

Early Pleistocene.—The culmination of glaciation marks this period. Matthew's map does not show the area of maximum glaciation completely (cf. Hulten, 1937). During early Pleistocene the Black, Caspian, and Aral seas were united into the huge Hyrcanian Sea. Asia Minor and the Balkan Peninsula were continuous land. The Mediterranean was separated into two closed seas, i.e., there was one land connection across the Straits of Gibralter and another connecting Tunisia, Sicily, and Italy. Africa was again connected with Asia by all of Arabia. These facts are all of significance in connection with the present distribution of *Crepis*.

RELATIVE AGES OF THE THREE CHIEF MOUNTAIN SYSTEMS OF ASIA AND THE MOST PROBABLE REGION OF ORIGIN OF *CREPIS*

In the following discussion no pretense is made to a critical analysis of the many problems connected with the relative ages of individual mountain ranges in Asia. Some of these problems are discussed by the various authors represented by contributions in the *Structure of Asia*, edited by J. W. Gregory. Among these and various other authors cited, there seems to be general agreement on the thesis that there were three distinct periods of mountain building in this continent; and, by a brief review of these different periods of orogenic activity and their chief results, it is hoped to throw a little more light on the problem of the general region of origin of *Crepis*, particularly whether it was more probably in the northern, central, or southern part of Asia.

The oldest mountains in Asia are the remnants remaining of the so-called "primitive nucleus" of Suess (1901) or the "archaic old vertex" of Fickeler (1925). The western, southern, and southeastern margin of this region is indicated by the line of dots and dashes in figure 8. This U-shaped range, situated in what is now the Lake Baikal region of Siberia, was upfolded as early as the Paleozoic era (cf. F. E. Suess, *in* Gregory, 1929, p. 36); and it may well have played an important role in the early history of the evolution of higher plants in Asia by providing new types of environment. Such an inference is in keeping with the views expressed by Seward (1941, p. 279), as follows: "The rich plant beds of Siberia, which include Carboniferous, Permian and Mesozoic strata, are still very imperfectly known. The more we know of the plants preserved in the older Permian rocks and in the beds classed as Permo-Triassic in China and Korea, the more promise there seems to be of discoveries which will enable us to reconstruct some of the missing links in the chain of plant life connecting the Paleozoic and Mesozoic floras. There are indications that the original home of many genera characteristic of the earlier Mesozoic vegetation may have been in the continent of Angara (=northeastern Asia), a region which has been preëminently immune from the disastrous consequences of geological revolutions." And, again (*op. cit.*, p. 290): "The late Paleozoic vegetation derived its characteristic features from floras composed in great part of extinct types, whereas among the plants of the late Triassic floras we at once recognize the precursors of more familiar and more modern forms. The preliminary steps in this transformation were taken in the latter part of the Paleozoic era." This view agrees with that of Gothan (1930), who points to eastern Asia as the region of origin of the flowering plants.

These general ideas of Seward and Gothan concerning the importance of Angara as a region for the development of new floras during the Mesozoic and Cenozoic eras have been supplemented by Kryshtofovich (1933) in his study of the Baikal formation of the Angara group. Through the kindness of M. K. Elias, who translated parts of this paper for me, the following brief generalization is a dependable statement of Kryshtofovich's views: (1) In Permian time certain elements of the Gondwana flora moved into more northern latitudes. In Asia they mingled with elements of the European flora which had become changed under the influence of desiccation; and together these gave rise to the Mesozoic flora of Angara. (2) In mid-Cretaceous time the composition of the flora of Angara continent radically changed. This new Cretaceous vegetation, the Angiosperms, probably came from the north. That they had a circumpolar distribution is shown by the existence of systematically and biologically similar forms in the floras of the Potomac region (eastern United States), of Souchan (Russian Far East), and of Portugal. (3) Be-

tween early and late Cretaceous there occurred a great oceanic flooding of Angara continent from the east and, when parts of the continent once more rose above sea level, they were populated anew by an entirely different flora in which the Mesozoic relicts were, for the most part, exterminated. A temporary marine transgression

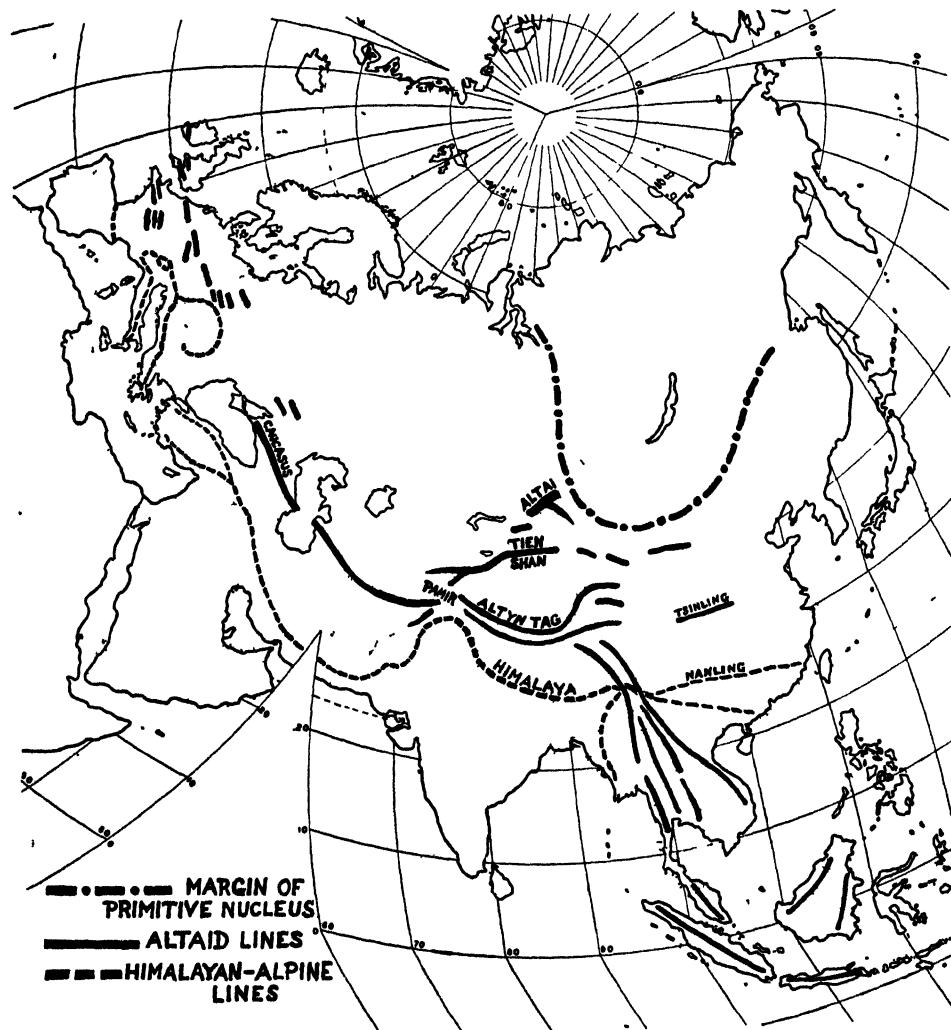


Fig. 8. Diagrammatic representation of the three principal systems of mountain chains in Asia, the Primitive Nucleus, the Altaids, and the Himalayan-Alpine system, and the extensions of the last two in Europe. (Copied from fig. 2 in Gregory's *The Structure of Asia* with slight modification.) Based on Goode *Base Map No. 201 PC*. By permission of the University of Chicago Press.

could not possibly cause the evolution of new forms of plant life; but it was sufficient to eliminate some species of plants, thus giving space for others, creating new edaphic conditions, and eliminating competitors in the struggle for existence.

Although the primitive mountain nucleus of northern Asia may have been an important factor in the *early* evolution of the floras of the present day, yet it can hardly have been so important in the middle and later periods of that long continuum. By the middle of the Paleozoic era these mountains, according to Barbour

(in Gregory, 1929, p. 195), were already greatly reduced. Since erosion probably continued throughout the Mesozoic era, by the dawn of the Tertiary period they must have been relatively unimportant topographically.

The next important mountain-building period in Asia produced the western Altai and Tien Shan mountains, several nearly parallel east-west ranges lying to the south and southeast of the Tien Shan-Fergana system, also a series of ranges extending eastward from Tien Shan, and several nearly parallel chains running southward from eastern Tibet and western Szechuan through the Malay Peninsula, as well as the Ural and Caucasus mountains, and the Variscan and Amorican horsts of Europe. These Altaid systems are shown by solid black lines in figure 8. Recurring movements were involved in the formation of these mountains. These movements began toward the end of the Paleozoic era and recurred from time to time through the Mesozoic era (cf. Cotta, 1871, p. 299; Fickeler, 1925, pp. 173-181; Nekhorosheff, 1932, pp. 23-24; Karakin and Korniliev, 1935; Javjarov, 1935; Murchison et al., 1845, pp. 408, 464; Volkson, 1940). Each of these great systems has a complex history, marked by epeirogenic movements alternating with periods of rest. For example, Berkey and Morris (1927, p. 314) discuss the history of the Artsa Bogdo Mountains, an eastern extension of the Altai range. They conclude that this part of the Altai system was uplifted and peneplaned during or before Lower Cretaceous time. They also report evidence of faulting and tilting, recurring since that time at such long intervals that the relief features due to faulting were planed away. Nevertheless, unlike the almost completely eroded Variscan and Amorican horsts extending across middle Europe from west to east, which correspond in age with the Altai and Tien Shan, these mountains of Central Asia still rise to great heights (up to 4,500 meters in the Altai and to nearly 7,000 meters in the Tien Shan) and contain many glaciers. According to Fickeler (1925, p. 174), the Russian Altai has remained a part of the Asiatic continent from the Carboniferous period to the present time (see also Murchison et al., 1845, p. 499). The combined effects of epeirogenic movements and erosion have left the highest points in the original fault-mass ranging from 2,000 to 2,300 meters high in the Russian Altai and from 2,000 to 3,700 meters in the Mongolian Altai. Furthermore, the same author (*op. cit.*, pp. 176-177) states that the Altai was twice as high in the Paleozoic era as in the Tertiary period. Even in the Mesozoic the elevation of the Russian Altai must have been 5,000 meters. Tertiary tectonic processes brought new climatic relations, resulting in the contrast between the central dry region (Mongolian Altai) and the peripheral humid region (Russian Altai). Superimposed on this great contrast were still greater climatic variations. For example, in the South Altai a subtropical flora is found in Lower Pliocene deposits. Fickeler concludes (*op. cit.*, p. 182) that in the Altai living things find a starting point. Plant geography shows it to be the native home of a flora that radiated far into Europe, a flora of which gigantic representatives still charm the eye of explorers in the Altai, whereas to Europeans, only their dwarfed forms are known.

Thus it has been possible for the Altai to serve as a favorable region for the continuous evolution of plant phyla at least up to Pleistocene times when heavy local glaciation may have destroyed some, but not all, of the alpine autochthonous species which had not already migrated southward. In this connection I am indebted to C. W. Sharsmith for pointing out the basic fact "that glacial phases are the most favorable climatically for the flourishing of true alpine (or arctic) species in the region of origin, where areas free of ice occur." For this reason, further exploration of the Altai-Tien Shan Mountains will probably reveal other primitive

species of *Crepis* as well as *Dubyaea* and *Soroseris* (see p. 82). The point to be emphasized here is that in northern Central Asia there was available all through the Tertiary period a region of highly diversified topography and a temperate climate where the ancestors of the Cichorieae could have developed and produced such primitive Cichoriaceous genera as *Dubyaea*, which in turn produced the most primitive species of *Crepis* and numerous other genera.

The third great mountain system lies to the south and consists of the Nanling, Himalayan, and associated ranges, which correspond roughly in age with the mountains of Iran, Asia Minor and the Balkan Peninsula, the Alps, and the Pyrenees. These mountains are indicated by lines of short dashes in figure 8. This series of high ranges was formed during a long period of vast orogenic activity, including volcanic eruptions which began mostly in Oligocene. By mid-Miocene some of these great ranges, for example the Alps, were fairly well developed; but the general process of mountain formation along this great axis continued throughout the Pliocene and into Pleistocene or even Recent times. According to Schwarz (1938), the Himalayas were elevated in late Pliocene and Pleistocene and the Pamirs and Hindu Kush and the mountains of Asia Minor even later. Regarding Asia Minor, Syria, and especially Iran, however, it has been shown by Böckh, Lees, and Richardson (in Gregory, 1929, Chap. III, pp. 153-168) that orogenic movements began in this region as early as the Paleozoic era and that the main movements occurred in Pliocene times. From this it follows that most if not all of these mountains of the south, from the Nanling-Himalayan system to the Alps and Pyrenees, were in stages of development suitable for colonization and migration by plants being driven southward by increasing cold during Pliocene.

But the relic species of *Dubyaea* and *Soroseris*, which are endemic in southeastern Asia and the western Himalaya region, probably spread into those regions from Central Asia early in the Miocene epoch, if not earlier (cf. Stebbins, 1940, pp. 73 and 75). According to Stebbins (*op. cit.*, pp. 51-52), these primitive relatives of *Crepis*, like many other relic alpine species of southwestern China and eastern Tibet, appear to be remnants of a flora which was formerly more widespread but was largely destroyed by Pleistocene glaciation. Most of the relic *Dubyaea* species now occur, with many other relics, on or near the Altaiid mountain ranges of eastern Tibet and western Szechuan. *D. hispida* is distributed westward through the Himalaya, but this probably resulted from post-Pleistocene dispersal. Stebbins (*op. cit.*, pp. 52-53) also points out that *D. oligocephala*, another primitive species, like *Soroseris Gillii* subsp. *occidentalis* and *S. Deasyi*, occurs only in the western Himalaya and adjacent regions, and that this disrupted distribution between closely related species of southwestern China and western Himalaya is characteristic of a number of genera (cf. Diels, 1913). Most of the *Soroseris* species have a wider distribution than the *Dubyaea* species, either in southwestern China, or in western Tibet, the western Himalaya, and Sinkiang. Thus, the distribution of the genus *Soroseris* as a whole (cf. Stebbins, *op. cit.*, p. 54, fig. 14) may logically be interpreted as indicating a Central Asiatic origin and center of distribution. In this connection it should be noted that *S. Deasyi* apparently exists now in the middle Tien Shan Mountains. One herbarium specimen (*Deasy* 95, BM, UCf) has only "Aksu" and "5000 m" on its label. But the town of Aksu is at an elevation of only 1,000-1,500 meters, whereas the Aksu River just to the north rises in the middle Tien Shan. Since the other four elevations at which this species is known to occur are all over 4,000 meters, it is much more likely that this specimen was collected in the high mountains than on the plateau. To the present author, one collection of a single *Soroseris* species in the Tien Shan Mountains is very significant, since it

shows that one of these relic species now exists in the region assumed, on other grounds, to be the center of origin of *Crepis*.

The nine species of *Crepis* now known from the Sino-Himalayan region represent but four different sections (8, 17, 18, and 21), only one of which, section 18 with five species, is well developed in this area. The other four species certainly appear to have migrated into this region from elsewhere (cf. Stebbins, 1940, p. 73); and it is highly probable that all nine of these species, or their ancestral forms, followed the same general route from the Altai-Tien Shan region as that taken by the ancestors of *Dubyaea* and *Soroseris*. Referring again to figure 8, it is clear that the Altai mountain ranges radiate in a general southeasterly direction to the Malay Peninsula, thus providing a route from Central Asia to the present locations of most *Dubyaea* species; also that the congested series of ranges between the Tien Shan and the Himalaya would provide ample opportunity for the dispersal of wind-borne seeds. All in all, the present distributions of *Dubyaea*, the genus representing the ancestors of *Crepis*, and of the closely related genus, *Soroseris*, fit in perfectly with the hypothesis that the center of origin and dispersal of *Crepis* and its ancestors was in Central Asia.

THE DIVERSE TERTIARY FLORAS OF ASIA AND EUROPE

Kryshtofovich (1929), in discussing the evolution of Tertiary floras, shows that the Tertiary floras of eastern Europe and Asia belong to different floristic provinces. The principal floristic boundary line, he states, runs across northern Europe from southeast to northwest, separating the temperate flora of Arcto-Tertiary composition on the north from the subtropical and tropical flora of southern Russia, Ukraine, and the rest of Europe. The Crepidinae and the whole tribe Cichorieae are temperate and arctic, not tropical, lowland species. One would not think of tropical, early Tertiary Europe, therefore, as the region of origin of this group of plants. Kryshtofovich separates the Tertiary-Temperate region into the western Greenland Province, which includes the north Ural Mountains and probably adjacent Europe and Asia, and two great eastern provinces. One of these, the North Siberian Province, included northern Alaska. According to Kryshtofovich, the flora of this province shows resemblance to the older Greenland flora as well as to the earliest Cretaceous flora of the Laramie type found in Amur and Bureja; and of the latter it is clearly a descendant. In this connection Kryshtofovich remarks that, in parts of Asia, plants seem to have developed without interruption since they started from their primeval Cretaceous prototypes. The other great Asiatic temperate region recognized by Kryshtofovich as having existed during Tertiary is the Turgai Province, the vast "middle zone" of northern Turkestan, Siberia, Manchuria, Korea, Sakhalin, and Hokkaido, also most of Alaska and probably Arctic America and Greenland. It should be noted that although Chaney (oral communication) is not convinced that two distinct northern Asiatic Tertiary provinces should be recognized by different names, yet this "major classification of the Tertiary vegetation of Eurasia by Kryshtofovich" has been accepted by Chaney and Hu (1940, p. 109).

During the first half of the Tertiary age, at least until Lower Miocene, this region was covered with a uniform, deciduous forest in which amentiferous species predominated. Interestingly enough, many of the primitive *Crepis* species are found today associated with amentiferous trees; such species as, for example, *C. geracioides*, *C. lapsanoides*, *C. kashmirica*, *C. lyrata*, and *C. mollis* are known to be associated with such trees. Although this proves nothing, still it does show that some species of *Crepis* could have evolved in just such an association. Furthermore,

the Turgai Province area includes the western part of the Altai Mountains, which certainly existed throughout the Tertiary and which was a region of great diversity in topography and climate. Regarding the general trend of the climate in Central Asia during the Tertiary period, Chaney (1935, p. 96) has made the suggestion, based on a comparison of Miocene floras from western Siberia, the Altai, and southern Russia, that there was a gradual reduction in rainfall and probably in temperature in this region throughout the whole Cenozoic era.

TRENDS OF TERTIARY PLANT MIGRATION IN ASIA OF SIGNIFICANCE FOR CREPIS

The combined evidence from fossil plants and the geographic distribution of living species shows that during the Tertiary period there were four major routes of plant migration in Asia. One of these routes connected the region of northern Central Asia and North America by way of the Beringian land bridge. Over this route there was intermigration between the two continents; but the northeasterly trend from Central Asia into North America was undoubtedly the direction followed by *Crepis*. Another movement was a general southeasterly one from northern and Central Asia toward Korea, Japan, China, and the Malay Peninsula. Still another trend was in a southwesterly direction from Central Asia into southern Europe and northern Africa. Later in its beginning than the other three was the westerly migration from Central Asia across the steppes south of the Ural Mountains into northeastern Europe. These four distinct migration trends are indicated on the map in figure 9. The pointed directional lines are intended merely to show the general direction of what must undoubtedly be thought of as radial mass movements from the general region of Angara and Central Asia. No pretense is made here to a complete review of all the available evidence bearing on this vast subject. But it is hoped that in the following discussion sufficient evidence will be presented to warrant the foregoing generalization and to provide a dependable background for the hypothetical history of *Crepis* which has been based mainly on phylogenetic and distributional evidence.

The northeasterly trend from Angara and Central Asia.—Recognition of an important trend of plant migration from northern Asia can be made without definite commitment with respect to the actual region of origin of the species involved. As was indicated by Seward (1941) and Kryshtofovich (1933), the ancestors of the Tertiary arboreal and herbaceous species of the Northern Hemisphere may have originated in Angara. But in the latter part of the Cretaceous period both Eurasia and North America were elevated and became continuous with the Arctic Continent (fig. 5, map 1). This could have made possible the holarctic distribution of many conifers, of which *Sequoia* is an outstanding example (Chaney, 1940), and such primitive angiospermous trees as *Magnolia*, *Platanus*, and *Quercus* (Seward, 1941, pp. 389-391), and *Cercidiphyllum* (Chaney, 1938, pp. 377-378). By middle Eocene, however, both Europa and Angara were once more completely insulated (fig. 5, map 2); and it was not until mid-Oligocene that Arctica was again lifted above the sea and that Asia was again united with North America. Hence, it seems much more probable that it was in mid-Tertiary time that such warm temperate genera as *Cedrus* and *Datisca* must have migrated from Asia into North America. That this was the direction of migration, rather than vice versa, is certainly indicated by the present distributions of both genera which resemble that of *Crepis*.

Schwarz (1938) explains the present distribution of the genus *Cedrus* as due to the interrelations of diverse old floras which met in the Mediterranean region. Nevertheless, the distribution of the four species appears to the author to be con-

sistent with the assumption that the genus originated in northern Asia; *C. deodara* in northwest Himalaya, Afghanistan, and northern Baluchistan; *C. libanitica* in southern Asia Minor and Liban; *C. brevifolia* in Cyprus; and *C. atlantica* in Algeria and Morocco. Furthermore, such fossil evidence as exists is not necessarily inconsistent with this assumption. According to Pilger (1926), *Cedrus* fossils have

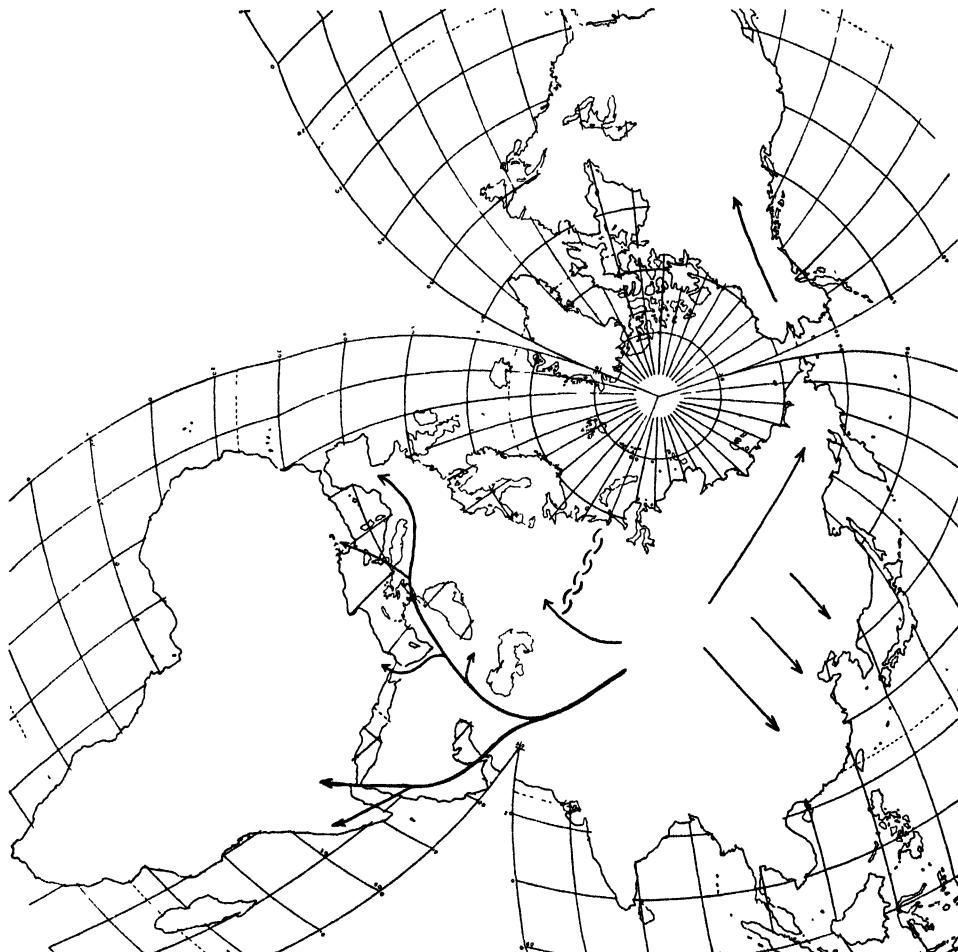


Fig. 9. Map showing the four trends of Tertiary plant migration of most significance for *Crepis*: (1) northeasterly from northern Asia into North America; (2) southeasterly from northern Asia; (3) southwesterly from Central Asia across the southern end of the Ural Mountains into southern Europe and northern Africa; (4) westerly from Central Asia across the southern end of the Ural Mountains into northeastern Europe. Fossil evidence shows that all of these trends, except the fourth, began before the assumed migration period of *Crepis*; and *Crepis*, like many other younger groups, followed similar routes. Based on Goode Base Map No. 201 PC. By permission of the University of Chicago Press.

been reported from Cretaceous deposits in western Europe and from Tertiary deposits in France and Germany, as well as in eastern Siberia. The last-mentioned locality, from the original report (Heer, 1878), is actually in south-central Siberia, about 100 kilometers west of Krassnojarsk. There, in a Miocene deposit, were found cone scales, seeds, and leaves of a species which Heer states is undoubtedly closely related to *C. deodara*. Recently, well-preserved specimens of *Cedrus* wood have

been discovered in Tertiary auriferous gravels in California (Barghoorn and Bailey, 1938). The wood in these specimens, being neither mineralized, nor lignitized, nor carbonized, can be distinguished from that of existing species of *Cedrus* by the absence of ray tracheids; and a similar difference exists between certain fossil pines and existing species.

Although it must be admitted that the oldest known fossils of *Cedrus* are from western Europe, yet similar or older records may eventually be discovered in Asia. One thing is certain, that during Tertiary the genus was distributed in Europe, Asia, and North America. Furthermore, in an extensive review by Schwarz (1938) it was concluded that such arboreal genera as *Cedrus*, *Pinus*, and *Quercus* represent the primary Mediterranean flora which came from Asia (see p. 106). A similar inference is drawn by Markgraf (1934, p. 71) concerning the Asiatic origin of certain species of *Pinus* and *Picea*. Thus, it appears that northern Asia or adjacent Arctica may be considered as the probable region of origin for *Cedrus*. This is in line with the general conclusion of Seward (1941, pp. 387, 400) that the origin of the conifers of the Northern Hemisphere was in the arctic region. From the known fossil record of *Cedrus*, it would appear to have originated in the Asiatic rather than the American Arctic.

In her critical study of the problem of the Pontide (a hypothetical land connection across the Black Sea joining Asia Minor and Crimea), Czeczott (1937) points out that the heavy rainfall which occurs in northern Anatolia and the absence of barriers against plant migration across northern Asia Minor are of great importance in explaining present-day plant distribution in that region and to the west. The problem of the Pontide is of only minor significance for *Crepis*; but some of the studies of the Colchic-south Euxine plants made by this author are very convincing in respect to the plants having an Asiatic origin and having migrated both eastward and westward. Among these are *Datisca cannabina* and *Fagus sylvatica*.

Although the other genera of the Daticaceae inhabit tropical India and the Sunda Islands, *Datisca cannabina* is a temperate species, occurring up to 3,000 meters altitude. This species is found not only in Colchis (the district at the eastern end of the Black Sea and south of the Caucasus) but also at isolated stations in southern Asia Minor, Syria, and Crete, as well as in northwestern Persia, Afghanistan, eastern Turkestan, Kashmir, and India. Czeczott points out that the Colchic flora is inseparable from the sea; and, therefore, it must be assumed that these inland stations were situated near a sea at some past epoch. It is known (cf. Moshketov, *in* Gregory, 1929, pp. 177, 185) that in eastern Turkestan (Ferghana) the sea lasted until Upper Oligocene times. Ancient Tethys persisted from Cretaceous to Oligocene and extended across western, northern, and central Persia. During Lower Miocene, when lagoon conditions set in and formed thick beds containing salt and gypsum, extreme desiccation took place (cf. Gregory, *op. cit.*, Chap. III). In Upper Miocene, only a narrow gulf penetrated into central Persia from the Persian sea (*ibid.*, Chap. VIII). From this evidence Czeczott infers that the gap between the eastern and western parts of the distribution of *Datisca cannabina* resulted from the dryness of the climate in the Miocene epoch and that this species is not younger than Upper Oligocene. This she states is confirmed by the fossil remains found between Turgai and the Aral Sea which are considered as Oligocene deposits by Abich and Kryshtofovich. The survival of *D. cannabina* from that remote period is correlated with the plasticity shown by its great vertical distribution, from sea level to 2,000 meters in Colchis and from 300 to 3,000 meters in Kashmir. Finally, the only other species of this genus, *D. glomerata*, is found in California and Mexico, occurring up to 1,500 meters altitude in the California

mountains. Like *D. cannabina*, it is a temperate, not a tropical species. These facts concerning *D. cannabina* and its closest relatives certainly indicate a Central Asiatic origin for the group.

Fagus sylvatica L., the common beech, is one of the Colchic-south Euxine trees mentioned by Czeczott as abundant and aggressive in that region. The general distribution of this species includes—in addition to northern Anatolia, Pontus, and Lazistan—the Persian province of Astrabad, southeast of the Caspian Sea; also it is widely distributed in middle Europe and in southern Europe—in northern Greece and Albania, Istria, the southern base of the Alps, the Apennines, Sicily and Corsica, southern France in the Cevennes Mountains, the eastern Pyrenees, and northern Spain. In the southern Balkan Peninsula and in the Pyrenees this tree has associated with it such primitive *Crepis* species as *C. geracioides* and *C. lapsanoides*.

Fagus is one of the many genera which are much older than *Crepis*, but which appear to have originated in Asia or the Arctic region to the north of the present continent of Asia, and which seem to have followed a developmental and migrational history somewhat similar to that of *Crepis*. Even though *Fagus* were holarctic in distribution at one time, this does not preclude its having originated in Angara or adjacent Arctica. The other existing members of the genus *Fagus* are *F. Sieboldii* and *F. japonica* of Japan and *F. grandifolia* of eastern North America.

According to Prantl (*in* Engler u. Prantl, 1894, 3[1]: 53, 54) various fossil forms of *Fagus* are known in Cretaceous and Tertiary deposits; and some of them extend the earlier distribution of the genus to Alaska, Washington, Oregon, and California, as well as to Spitzbergen, Iceland, and Greenland. Without a critical study of adequate fossil specimens of both this and related genera, it would, of course, be impossible to determine whether *Fagus* originated in Angara or Arctica. Kryshtofovich (1935), however, describes *F. Antipovii* as "definitely archaic," and this is one of the characteristic species of the Tertiary flora that covered the vast region extending from northern Turkestan and southern Siberia eastward. This fossil species has also been found in Alaska. It is true, therefore, that primitive forms of *Fagus* were distributed continuously across Siberia and North America to Greenland and Iceland late in the Cretaceous period. It has been shown by Kryshtofovich (*op cit.*) that *Fagus Antipovii*, like many other species of the temperate Tertiary Siberian flora which developed during late Cretaceous in Asia and possibly in the Arctic, migrated westward and southwestward, reaching Europe during the Miocene epoch.

In their studies on the Pliocene flora of Bulgaria, Stefanoff and Jordanoff (1935) found the Fagaceae second only to the conifers in relative abundance. *Fagus orientalis* Lipsky, the fossil beech which they found, is believed to be the parent form of *F. sylvatica* L., the common beech of today. It, therefore, may be considered, at least in a general sense, as a connecting link between the latter and certain more primitive species, like *F. Antipovii* of Siberia and Alaska.

Thus, the distribution of *Fagus* in Tertiary times indicates a history of development and migration in general similar to that of *Datisca cannabina*, the salient features of which are probable Asiatic origin and migration eastward into North America and westward into Europe. That these features also characterize the history of *Crepis* will be made clear in chapter 8.

The southeasterly trend from northern Asia.—That the southeasterly trend of Tertiary floral units across both Eurasia and North America is an expression of continental essentially like that now controlling the distribution of living forests in the Northern Hemisphere was first pointed out by Chaney (1940). Chaney and

Hu, in their study of a Miocene flora from Shantung Province, China, find "evidence of a southward-migration of the temperate forest in eastern Asia corresponding to that between Alaska and Oregon between Eocene and Oligocene." They also cite other evidence supporting a "southward movement of vegetation during the epochs following the Eocene" in eastern Asia. They attribute this "migration of the temperate flora from high northern to middle latitudes by Oligocene time" to geographic changes involving "the draining of the Obic Sea which connected the Arctic Ocean with Tethys during the Eocene, and perhaps the withdrawal of other meridional seas which had facilitated the transfer of warm waters into high latitudes." With the further great reduction in size of Tethys from Miocene to Pliocene, it is safe to assume that this north-south trend of migration of vegetation in Asia extended farther westward. The significance of this migration trend for the history of *Crepis* has already been indicated (p. 97) in the discussion of the present distribution of the supposed ancestors of *Crepis* (or their living representatives) in the mountains of southeastern Asia.

The southwesterly trend from Central Asia.—The importance of this trend in Asiatic-European plant migration was fully appreciated by Engler (1879). In his detailed treatment of the development of the high montane flora before, during, and after the glacial period, he derives among others the following generalizations. (1) The genera represented by alpine and high alpine species in the Himalaya are for the most part the same as those represented by alpine species in the Pyrenees and Alps. (There are five primitive *Crepis* species which occur only in the Alps and the Balkan Peninsula; whereas there is none which occurs only in the Altai. But several of the most primitive species, namely, *C. sibirica*, *C. chrysanthia*, *C. lyrata*, and *C. conyzaeifolia* occur in the Altai; and their distribution indicates that they were dispersed from the Altai.) (2) When the few representatives occurring in the Alps also occur in the Altai, in addition to relatives of the same group, their origin in Asia is decided. (Of the four *Crepis* species mentioned above as occurring in the Altai Mountains, *C. conyzaeifolia* also occurs in the Pyrenees and the Alps as well as in northern Asia Minor, Transcaucasia, and northern Persia. *Crepis* is also represented in the Alps and Pyrenees by other primitive species and in the Himalayas by four alpine species, one of which, *C. kashmirica*, is one of the most primitive species in the genus.) (3) Worthy of greatest consideration is the fact that, of the plants of the Altai and other parts of Siberia, several, such as *Aconitum anthora*, *Saussurea discolor*, and *Pedicularis comosa*, certainly occur in the Alps and Caucasus, but not in Scandinavia. This shows that part of the plants that migrated from Siberia to the Caucasus and Alps went apparently in a southwest direction to the Mediterranean mountains and not through Scandinavia. This land, at least at the height of the glacial epoch, was not suitable; otherwise, since there were high arctic plants that migrated to the Caucasus, Carpathians, and Alps, some at least could have existed in Scandinavia, as some do today as far north as the eightieth meridian. (This explanation of Engler's is inconsistent with his statement [below] that he knows of no evidence for as great glaciation as in the Alps; but it in no way detracts from the cogency of his evidence in support of the southwesterly migration from Central Asia.) The other Siberian glacial plants that occur in the western Alps, eastern Alps, and Carpathians appear mostly in the eastern Alps and Carpathians as a result of the first colonization by Siberian plants. (This "first colonization by Siberian plants" was apparently hypothetical on the part of Engler. Strong evidence that it actually occurred has been reported by Kryshtofovich [1935].) (4) From the distribution of the plants of the Altai and alpine Himalaya we can generalize concerning the migrations that went on in Central Asia. In the

Himalaya as well as the Altai the same genera occur; and the number of species in *both of these two regions* generally is smaller than the number of species that occur in *both* the Mediterranean mountains (including the Alps) and the Altai. The mountains south of Altai connecting the Altai with the Himalaya have developed their endemic montane flora from the steppe elements of the lower regions, as have the mountains of the Mediterranean peninsula. On the Pamir plateau and on Tien Shan, glaciation probably had a great effect, as it also probably did in the northwest Himalaya. But Engler states that he knows of no evidence, and this has been verified by others, for as great glaciation as in the Alps (cf. map of maximum glaciation of Hulten, *op. cit.*; also Cotta, 1871; Karakin and Korniliev, 1935; Javjarov, 1935). Fewer areas were therefore opened for colonization than in the Alps (this obviously applies to *Crepis*). The actual migrations of the flora from Afghanistan, Persia, and Turan occurred after Miocene time, when moisture gradually decreased and the climate became drier. Western Asia became the reservoir of relic mesophytic vegetation and, gradually, more and more steppelike. Steppe animals occurred in the higher parts throughout the whole region and could easily have carried seeds from Altai to Himalaya and from these mountains to western Tibet, Afghanistan, Turan, Songoria, and Ala-Tau; but here, according to Engler, because it would not be so easy for the seed to produce progeny, the terrain generally developed nearly related forms (referring presumably to the origin of vicariant species from the original migrants); whereas north from the Caucasus, the Carpathians, and the Alps, the plants growing in longer summers, through their retreat to the south or by complete extinction, gave place to the species coming from the east.

Some of Engler's ideas on the migration of high montane plants, further elaborated in a much later publication (Engler, 1916), are so applicable to *Crepis* that they will be mentioned here.

1) The assumption that vicarious species remnants represent former polymorphic types with a wider continuous area finds an obstacle when it concerns species with claims to special climatic and ecologic relations and which occur only in high mountains that are separated by wide plains or seas. There are two possibilities: (a) An older long since extinct stem species has lived at the foot of the mountain area in Tertiary; and at different points in its area, with conditions sometimes varying and resembling those in high mountains, mutations have resulted in parallel forms or vicarious varieties which developed into species. (b) Seeds of species A, growing under high montane conditions, were spread by birds or winds from mountain to mountain; and in the new locations there occurred mutations, $A' = B$, $A' = C$, which remain as relic species.

2) From polymorphic types, groups of species are gradually developed which are, ecologically: (a) groups in which there are forms at present in hilly country with a short winter near higher regions with a long winter; (b) groups containing only species in regions with a very long winter and short summer. From old Tertiary elements of the lower regions, by successive mutations, new species were formed at the upper limits which have passed into higher regions with harsher climates.

3) For the hypotheses of plant migration in general, the transportability and length of vitality of the seeds are to be considered, as well as the climatic conditions under which a group of species flourishes today. (With reference to *Crepis*, these points are discussed in chapter 8.)

4) For the estimation of the possible migrations in the glacial period and especially for the preservation of species in areas subject to glaciation, it is not unimportant to know how high species go up in the higher regions and how low they

come down in the lower regions. (All available data on the altitudinal range of *Crepis* species will be found in Part II; see also the altitudinal distribution of the endemic species of *Crepis* in the following chapter.)

Engler's conviction concerning the derivation of important elements in the high montane flora of southern Europe through southwesterly migration from Central Asia have been corroborated by Braun-Blanquet (1923). Braun-Blanquet's reply to the question whether our representatives of the original flora of the Alps migrated into the Alps unchanged is that *phylogenetic and phytogeographic research compels the question to be answered unconditionally in the affirmative*. The Tertiary basic stock of the alpenflora, according to this author, was derived chiefly from Mediterranean and middle Asiatic stems and migrated into the Alps partly from surrounding lower country and partly from neighboring older mountains. During the Pliocene age new endemic forms developed. In addition to the Mediterranean and middle Asiatic stems, three less important components are mentioned by Braun-Blanquet as contributing to the high montane flora of southern Europe. The northern flora, which came in from the northeast during the Ice Age, decreases in importance in the Alps from northeast to southwest. The Sarmatic flora (Sarmatia is the region north of the Black Sea), considered broadly, has contributed species which characterize the dry valleys of the coniferous zone in the central Alps. The west European or Atlantic flora is very scantily represented in the Alps in contrast to the mountains of middle France and the Pyrenees.

Similar conclusions had already been reached by Braun-Blanquet (1921-1930) as a result of his exhaustive study of the present and fossil floras of the mountains of central France, where he recognized three principal elements: the Eurosiberian-Boreoamerican, the Mediterranean, and the Aralo-Caspian. The first of these is subdivided into three subelements: the middle European, which is autochthonous, the Atlantic, and the Boreoarctic. Although his classification of the woody-stemmed species under these elements is presumably correct, it may be that future research on the herbaceous species will necessitate some changes. Of the five species of *Crepis* reported, for example, none is referred to the Eurosiberian element. It is very probable, however, that *Crepis paludosa* and *C. mollis* migrated from the Altai region into northern Europe and then spread west and south (see pp. 137, 139) and would therefore be referred to the Eurosiberian element. Of the other three species, *C. albida* is placed in the Mediterranean-montane element; whereas *C. lapsanoides* and *C. conyzaeifolia* are referred to the Aralo-Caspian element. Nevertheless, the synthesis of evidence on this genus shows conclusively that all three of these species must have migrated from western Asia by way of the Irano-Pontic-Balkan route (see pp. 140, 141).

Considering next a region far to the east, Korovin (1935) reports on the analysis of the present flora of Betpak-dala from the standpoint of its developmental history. This region is discussed here because the presence there of two fairly primitive species certainly indicates that the uplands were populated by *Crepis* in earlier times. *Crepis oreades* of section 11 is reported by Pavlov (1938, p. 368) to occur in the Ulutavsk (Ulu-Tau) Mountains near the Aral Sea, and in the mountains of southern Kazakhstan, north of Lake Balkash. This Central Asiatic endemic is also fairly common in the mountains from Altai to Pamir. *Crepis pannonica* of section 10 is found on the steppes of Turgai, close to Betpak-dala, and in the mountains of northwestern Persia. Two of the most primitive species in this section, *C. darvasica* and *C. songorica*, are endemic in certain mountains of Russian Turkestan (cf. fig. 10, 10-DA, 10-AT).

The desert of Betpak-dala is that part of northern Turkestan lying between the

Sary-Su River on the west and Lake Balkash on the east. It is part of the vast Kirghiz steppe region which also includes the Turgai province to the northwest. The more mountainous Semipalatinsk region to the northeast merges into the Altai mountain region on the east. Korovin states that in southern Betpak-dala the flora is characterized by young species of the Mediterranean element. But most of the region, like the other northern deserts of Central Asia, has a flora characterized by primitive types, the Kirghiz element. Species belonging to this element occur in Ust-Urt (between the Caspian and Aral seas), in northern Turgai, in Betpak-dala, around Lake Balkash, in the central Tien Shan Mountains, and in the Pamir-Alai Mountains. It has been shown by Nalivkin (1926) that late in the Mesozoic era this region was composed of isolated massifs like the Ural and the central Tien Shan. In Miocene time there had been added the plateaus of Ust-Urt, Betpak-dala, and Turgai. The earliest fossil traces of the Kirghiz element are associated with the uplift of the mountains in the Miocene.

The Kirghiz element, according to Korovin, was derived from two different sources. Some of the species are relics of the old African or Gondwana flora which reached the Kirghiz region during the Cretaceous epoch. The other source of the Kirghiz element was Central Asia (which includes the Tien Shan—Altai region). This evidence that the present xerophytic flora of the Kirghiz steppes was derived in part from the middle Asiatic source supports the thesis that in mid-Tertiary times there was a westward and southwestward trend of plant migration from the Tien Shan—Altai region.

Turning now to Asia Minor, we find that Schwarz (1938), in his extensive review of the literature bearing more or less definitely on the floristic history of this region, reaches some generalizations which are of marked significance in connection with the southwestward migration of *Crepis* from Central Asia. After noting the striking picture made by the flora of Asia Minor, with its accumulation of distinct but closely related species, its unusually rich mosaic of vicariants, and its multiplicity of adaptive, progressive forms, he states that we make no mistake if we consider the Turco-Iranian primary flora as a distinct and continuous branch of the original flora of Angara continent, a branch which from the beginning won its direction by orientation to the continental climate. To the present author there appears to be no reason why *Crepis* should not be considered a part, or at least a derivative, of this original Angara flora.

Further, Schwarz also concludes that part of this primary flora migrated into the Iberian Peninsula and into the Atlas Mountains; and, since the traces of this invasion consist mostly of single species of the same genera or sections, with vicarious relatives in the primary development center, this extensive migration must have been relatively ancient. The Miocene is considered to be the epoch during which it occurred, and, incidentally, it is noted that the Dinaric (Dalmatian) Alps were probably uplifted in early Miocene. From the existence of related but highly divergent species of various genera in Central Asia and Asia Minor, Schwarz concludes that the Armenian-Kurdish mountain region formed a temporary distribution barrier with the consequent development of formenkreise in various groups. But it seems that the disturbance was not so prolonged and the isolation was not so great as to make a strongly marked secondary development center, because, as shown by the vertical distribution, the flora was relatively labile. A similar situation is seen in the overlapping of this primary flora in the mountains of the Aegean Islands and of Greece—its coherence, at least in the higher regions, was preserved. (These ideas are especially applicable to certain groups of *Crepis*; cf. sections 4, 6, 10, and 11.)

Schwarz also considers the peculiarities of the floras of northern and southern Asia Minor. The northern border of the region has a true relic flora and many of the types are now found in eastern Asia. Also, Asia Minor is definitely an area of refuge for the arctotertiary element in the sense of Engler. Southern and western Asia Minor has a true Mediterranean flora. At the same time, because of the many refuge areas extending from the western Himalayas to Makaronesia,¹ with relic species belonging to the primary flora, one can assume no outstanding secondary development center. To estimate the age of this Mediterranean-Sindic (Indian) refuge flora is very difficult. Certain of the trees, such as species of *Cedrus*, *Pinus*, and *Quercus*, appear in Eocene, Miocene, and Pliocene formations in Europe. Since these trees and certain associated shrubs and herbs include *Angara* types, they must represent a definite west Eurasian development center for these elements in early Tertiary; and this may be assumed to be the oldest Angiosperm stem of the Mediterranean flora. There are traces of this primary Mediterranean flora in Makaronesia.

According to Schwarz, the Dinaric connection between Europe and north Africa (Dalmatia, Italy, Sicily, Tunisia) had great significance for the preservation and spread of the west Eurasian Tertiary flora. Among the species that came in from western Asia is *Laurentia tenella*, the present area of which, including Portugal, the Balearic Islands, Corsica, Sardinia, Sicily, Crete, Cyprus, and Liban, clearly marks the southern edge of the old Dinaric line, i.e., the original European-African contact zone, which dates probably from Pliocene time.

The immediate causes of decimation of the species comprising this primary (*Angara*) element of the Mediterranean flora are assumed by Schwarz to consist of rapid climatic changes which occurred in late Oligocene and early Miocene and again in late Pliocene and early Pleistocene (see also Handel-Mazzetti, 1909, p. 52). The elevation of the Dinaric range of the Alps provided new environments, especially for oreophytic types. Relic types from the old Tertiary western Eurasian primary flora also became fixed in the area north of the Alps (cf. *Crepis sibirica*). Furthermore, contacts were established during Miocene between the Mediterranean-Sindian, the Turco-Iranian, the old African, and the Euro-Sinic primary floras resulting in the Euro-Mediterranean secondary flora which was already well characterized in the Pliocene. This explains the presence of four *Cedrus* species in the Mediterranean area, the rich content of *Primula* section *Auricula* distributed from the Pyrenees to Bulgaria, and of section *Farinosa* from the Caucasus to the Balkan Peninsula, as it does also the presence of the primitive *P. frondosa*, etc.

Thus, we find that Engler's general hypothesis concerning the derivation of south European and Mediterranean relic species from Asiatic sources through a southwesterly migration trend from Central Asia is strongly supported by Schwarz's extensive review of the more recent literature in this field.

The comprehensive review of literature by Hagen (1914), which deals mainly with the floristic relations between the Mediterranean region in Africa and Asia, must be mentioned because of the significance of his conclusions concerning an important Tertiary plant migration southwesterly from Asia into the Mediterranean region. After reviewing the fossil Miocene-Pliocene flora of southern Europe, Hagen discusses the paleoclimate and floral history of the Sahara region. He concludes, with reference to climate in north Africa, that no prolonged desert conditions existed in the Sahara during Miocene-Pliocene; and even in the western part there was a generally moist climate. But the Pleistocene period brought extreme

¹ Makaronesia is a term used by several authors on vegetational history to designate the islands and archipelagoes of the eastern Atlantic—the Azores, Madeira, Canary, and Cape Verde Islands.

fluctuations. In Pluvial times, times corresponding to the Ice Age of alpine glaciation, the rainfall became so abundant that even in the western Sahara, during most of this period, many large rivers were formed. Also, corresponding with the longest interglacial period, a long drier period existed. In late Pleistocene and Recent times desiccation became gradually more pronounced.

With reference to floristic relations, it is noted that there are a few rather old species in both the Sahara and in Asia Minor which must be assumed to have had an Ethiopian origin. But there is a host of steppe and desert species in western and middle Asia which are represented in the Sahara by related species. The latter, according to Hagen, *must have originated in Asia, and one gets the impression that in earlier geologic times an actual wave of desert plants flowed from Asia into the Sahara and took possession of it.* Hagen also notes the existence of some peculiar endemics in the Sahara south of the Atlas Mountains, which probably had an early Mediterranean origin. But he considers almost all of the Saharan flora as Asiatic in origin. From a consideration of Tertiary-Pluvial relic species in north Africa, together with fossil evidence, our author concludes that there was a fairly broad littoral along the whole Mediterranean coast of north Africa during the Pluvial period, and south of this a steppe zone where all the Saharan xerophytic endemics could have been preserved. It is in this region that many of the advanced species of *Crepis* now occur, as well as several more primitive endemics.

Hagen next considers the relations between the floras of the Mediterranean-Near East region and the Ethiopian region. The rich endemic flora of Abyssinia consists of mesothermic species, some of which also occur on other high mountains in tropical Africa. In general, these endemics exhibit Mediterranean and Asiatic affinities. Engler's idea that such species "traveled by jumps," being borne by the wind or by birds, is accepted for these species, but it is emphasized that the route followed may have been partly over the sea. In this connection it may be noted that, according to Bailey Willis (oral communication), Africa was relatively flat until Middle Tertiary, when diversification began. From that time until mid-Pleistocene north Africa had for the most part a cool, moist climate. The latter part of the Tertiary would be the most likely period for the migration of *Crepis* from Asia to Africa. These species could have reached tropical Africa from southwestern Asia over either of two routes: (1) the Eritrean route, following the mountains of northern Persia, southern Asia Minor, Syria, the Sinai Peninsula, and a range of peaks along the Red Sea; (2) the south Arabian-Somaliland route, which can be traced from northwestern India, through Afghanistan, southeastern Persia, the border of southeastern Arabia, and Italian Somaliland. But from southern Arabia this route could have been through Eritrea, and this, with reference to the present distribution of *Crepis* in tropical Africa, seems more probable. In Pluvial times either of these routes must have been favorable.

Hagen also discusses the problem of floristic relations between the Mediterranean region and Makaronesia (the four groups of volcanic islands off the coast of north Africa). From the standpoint of *Crepis* history this is of minor importance and involves only the Canary and Madeira Archipelagoes. Hagen considers a former land connection of the Cahary Islands with Morocco as good as proved, as he also does the contention that a former connection with Madeira Island existed (see also Willkomm, 1896, p. 260, cited by Handel-Mazzetti, 1909, p. 51). But his conclusion that the separation of both groups from the mainland occurred about the middle of the Tertiary period places that event too early for the rather advanced species of *Crepis* which are indigenous there to have migrated overland. There still remains the possibility, however, that they were transported by wind or birds.

The westerly trend from northern Central Asia.—The discovery of “a final link between the Tertiary floras of Asia and Europe” (Kryshtofovich, 1935) certainly indicates that the temperate deciduous flora of the Turgai province, moving westward around the southern end of the Ural Mountains, reached eastern Europe in late Oligocene or early Miocene time. During the Miocene period this temperate flora became dominant in Russia, which had formerly had the same tropical flora that extended from the Atlantic coast (cf. Reid and Chandler, 1933, p. 71) across Europe and southern Asia to the Indo-Malayan region, where it exists today. Evidence of the advent of the Turgayan Tertiary flora into eastern Russia was discovered near Sterlitamak, southwest of the Ural Mountains (about 54° N., and 56° E.). The fossil record is abundant and convincing. It may be taken to signify that the migration of the Turgayan flora into Europe south of the Ural Mountains, after desiccation of the Obic Sea along their eastern slope, was accompanied by the gradual displacement of the older tropical flora in eastern Europe. Concerning this important event in the history of the European flora, Chaney and Hu (*op. cit.*, p. 103) state: “The delayed arrival of the temperate flora as the dominant element in western Europe seems to have resulted from the continuous marine climate there into the Oligocene epoch. By Miocene time only remnants of the Tethys Sea appear to have remained and the vegetation had largely taken on the temperate aspect of the floras farther east in Eurasia, where continental climate had prevailed during most of the Tertiary period.” The establishment of this migration trend from Central Asia into Russia through the Turgai region and south of the Ural mountains sets an important precedent for the explanation of some aspects of the present distribution of *Crepis*.

The conception that angiospermous plants had their early development in Angara and that many members of that primitive flora migrated westward into Europe in Tertiary times has been accepted by other Russian botanists. V. P. Maleev (*in* Komarov, 1941, p. 143), for example, in discussing the Tertiary relic plants of western Transcaucasia, recognizes as one category *the mesophytic relics* of the “Angarida flora (A. N. Kryshtofovich’s ‘Turgai flora’) among which representatives of its northern and southern branches can be distinguished.” This allusion to the northern and southern branches of that part of the Angara flora which existed in Turgai can only mean that this author accepts two migration trends from the Turgai region, a westerly one and a southwesterly one. Maleev (*loc. cit.*) also accepts the view that this mesophytic flora was distributed throughout the whole Mediterranean region during Upper Pliocene and now persists only in the moister parts of that region. Similarly, J. D. Kleopov (*in* Komarov, 1941, p. 255) and M. M. Iljin (*op. cit.*, p. 292) both refer to Kryshtofovich’s Turgai flora which migrated into Europe in mid-Tertiary. This evidence of a wide acceptance of Kryshtofovich’s conclusions concerning the development of a temperate flora in northern Central Asia and the westward migration of many of its component species strengthens the foundation of our hypothetical history of *Crepis*.

SUMMARY

The general bearing of the foregoing review on the probable origin, development, and migrations of *Crepis* may be summarized as follows:

- 1) Ancient northern Asia, Angara Land, had been a relatively undisturbed continent for many millions of years previous to the Tertiary period.
- 2) The western part of the Altai-Tien Shan mountain region had been available since long before the Miocene epoch as a suitable region for the development of *Crepis* and its ancestors.

3) The fossil Tertiary floras of Asia and Europe indicate that in early Tertiary all of Europe except northern Russia and Scandinavia was tropical, whereas the northern half of Asia was temperate and became increasingly continental in character. Furthermore, the flora of the Turgai province, which includes the western Altai-Tien Shan region, indicates identical associations to those in which some *Crepis* species occur today.

4) By early Miocene the continents had risen sufficiently so that the Tethys Sea was greatly reduced, leaving two east-west arms on either side of a broad peninsula extending from southwestern Asia westward as far as Italy and eastern France. Also, the Obic Sea, separating Asia and Europe, had either disappeared or dried up sufficiently so that plant migration could occur south of the Ural Mountains.

5) During the last half of the Tertiary and the Quaternary period a great mountain axis extending from southeastern Asia to the Pyrenees was in process of elevation. Many new topographic conditions were interposed in the development of floras. At the same time, there was gradual desiccation of the region extending from Central Asia across the Mediterranean and northern Africa, accompanied by many relatively shorter fluctuations in moisture and temperature. All these changes were conducive to increased speciation in many genera, including *Crepis*.

6) During the Tertiary period there were four important trends of plant migration in Asia, all of which were significant for *Crepis*.

a) The northeasterly trend from Central Asia began at least as early as the Cretaceous period and continued throughout the Tertiary period. It was in the early part of this long period that such genera as *Fagus*, *Cedrus*, and *Datisca* probably migrated from Asia into North America. The American species of *Crepis*, or their ancestors, must have followed the same migration route in later Tertiary time.

b) The southeasterly trend from Central Asia began in early Tertiary, and by Middle Tertiary time *Dubyaea*, the ancestors of *Crepis*, and *Soroseris*, a nearly related genus, had probably migrated from Central to southeastern Asia.

c) The southwesterly trend from Central Asia into Europe and Africa also began, no doubt, before the Cenozoic era; but during the Tertiary period this trend of plant migration became increasingly important as a result of the general southward movement of vegetation in Asia. Evidence from various sources is found to show that there was a vast movement of plant species from Central Asia toward the southwest, with a profound effect on the floras of Europe and Africa, especially in the Mediterranean region. Many genera of flowering plants, including *Crepis*, were spread from Asia into both Europe and Africa during this long period. Even the high montane *Crepis* species of southern Europe, or their immediate ancestors, are believed to have migrated from Central Asia.

d) The westerly trend from Central Asia into northeastern Europe began in late Oligocene or early Miocene time. The present distribution of some of the most widespread *Crepis* species is explained by this migration trend.

CHAPTER 7

ENDEMISM IN THE OLD WORLD SPECIES OF CREPIS THE DATA ON ENDEMISM IN CREPIS

SINCE THE TWELVE indigenous *Crepis* species of North America are all more or less widespread, they will not be included in this discussion of endemism in *Crepis*. It should be noted, however, that in each of the four most primitive American species there exists a 22-chromosome "diploid form" which has a narrow distribution and may properly be considered as endemic. From this and other evidence presented in detail in the monograph on the American species (Babcock and Stebbins, 1938), the conclusion was reached that all of the American species either migrated from Asia across the Beringian land bridge or were derived from Asiatic species which followed that route of migration in preglacial time.

From the evidence on geographic distribution which has been reviewed in the preceding chapters, it is clear that a Central Asiatic origin is indicated for this genus. In the course of this discussion reference was made to a number of endemic species. In the present chapter the data on restriction of distribution in the Old World species are examined for the purpose of determining the extent and significance of endemism for the history of the genus.

The term endemic, in its usual biological connotation, is applied to a plant or animal which is limited in its distribution to a single country, region, or area. Of equal or perhaps greater importance is the extent of the organism's actual range of distribution within the endemic area. In order to obtain more definite information concerning the amount and possible significance of endemism in *Crepis*, arbitrary limits were chosen. The upper limit was suggested by the fact that the primitive, relict species, *C. geracioides*, is known from three localities which are separated by a maximum distance of approximately 150 kilometers (94 miles). The lower limit (50 kilometers or 31 miles) was found to be sufficient to include the area occupied by such a local relict as *C. kilimandscharica*. In the classification of the endemic species, the term "narrow" was used when the maximum straight-line distance between the known localities of a species fell within the lower limit; when the maximum distance between the known localities exceeded the upper limit, the designation was "wider"; when the maximum distance fell between the two limits, those species were classed as "narrow B." It was found that there were so few species in the "narrow B" group that, for the sake of simplicity, the "narrow B" and "wider" groups were lumped together, thus recognizing only two categories, "narrow" and "wider," with the dividing line at 50 kilometers.

On this basis it was found that there are forty-eight species of *Crepis* for which the available data indicate a "narrow" distribution. Twenty-eight of these are known from only one locality, and the other twenty are known from two or more localities. Of the twenty-eight that are known from a single locality, twenty-four are known to the writer from just one collection; but the other four are known to have been collected several times at the one locality. Three of these four localities are mountain peaks in Greece; the other is the eastern promontory of Madeira Island. The twenty-four localities at which only a single collection has been made are mostly in regions which have been less thoroughly explored botanically, such as Asia Minor, the Caucasus, Turkestan, and tropical Africa. Many of these localities are in mountainous country and some are mountain peaks. Since many of the "wider" endemics are known to be very local in their distribution, and half of the "narrow" ones are known from two or more collections, it is fairly probable

that most of the species known from only one collection will turn out eventually to be, as here defined, actually "narrow." At any rate, the purposes of the present discussion can be better served by recognizing them as "narrow" than by ignoring them.

Classification of the rest of the *Crepis* species as endemic or not endemic was accomplished by defining a series of endemic areas and then by accepting as endemic only those known to be restricted to a single area. Many of these areas are widely recognized as rich in endemic species of plants. By this method 91 species were selected as "wider" endemics. This does not mean that these species are continuously distributed over a district more than 150 kilometers in diameter. On the contrary, these "wider" endemics are all more or less local in their distribution, even though a few are fairly abundant in certain districts. Thus, in *C. geracioides*, it happens that the three known localities are about 150 kilometers distant from one another; whereas *C. terglouensis*, another very primitive endemic, is known from at least twenty high alpine stations ranging from south-central Switzerland to central Tirol and Upper Austria, a distance of at least 350 kilometers. In marked contrast with these are such insular species as *C. cretica* and *C. canariensis*, which are abundant on the islands where they exist. A few species have been omitted which occur mostly in one endemic area but are also represented in another and hence, on a less restricted criterion, might have been considered as endemic. Interesting examples are *C. pygmaea*, a very primitive 12-chromosome species of Spain, the Pyrenees, the southwestern Alps, and northern Italy; *C. smyrnaea*, another 12-chromosome primitive species known from only three localities in southern Greece and western Asia Minor; *C. pontana*, the most primitive 10-chromosome species of *Crepis*, which occurs from the eastern Alps to the western part of the Balkan Peninsula; and *C. albida*, the next most primitive 10-chromosome species, which is polymorphic and is distributed from the Grand Altas Mountains, in Morocco through Spain, the mountains of southern France, and the Maritime Alps. It becomes difficult to determine where to draw the line if one begins to go beyond the limits of a single endemic area. But on this restricted basis there are still 133 endemic species, which is 72 per cent of the 185 Old World species.

These 133 species, together with section numbers, are listed on the left-hand pages of table 8. Other pertinent data are, in order, as follows: the endemic region (Roman numerals); the endemic area (Arabic numerals); the number of localities at which it is known to have been collected; its distribution class (as determined from map measurements of maximum distance between known localities); and the serial number. On the facing right-hand pages are given the serial number; the phylogenetic group of each species (whether most primitive [primitive A], less primitive [primitive B], intermediate, or advanced); its altitude class (alpine, montane, or low); its moisture classification (as occupying a moist, subhumid, or arid environment); its life-duration class (perennial or annual-biennial); its variability class (monomorphic or polymorphic); and, finally, its diploid chromosome number when that is known. (Only three of the species are polyploids, and in these the chromosome number, shown in italics, is the basic, not the diploid number.) By means of this system of classification it has been possible to derive some significant generalizations concerning the relations between phylogeny and endemism in *Crepis*. Before considering these relations, however, let us examine the distribution of the endemic regions and areas.

The distribution of the endemic regions and areas for Crepis.—The endemic regions and areas for *Crepis* are defined in table 9 and shown in figure 10. In this figure the large size of the tropical African area (no. 19) will be one of the first

TABLE 8
THE ENDEMIC SPECIES OF CREPIS OF THE OLD WORLD

Section	Species	Region	Area	Number of localities known	Distribution class	Serial number
1	<i>C. geracioides</i>	II	4	3	narrow B	1
1	<i>C. viscidula</i>	II	4	20+	wider	2
2	<i>C. kashmirica</i>	VI	11-HI	10	wider	3
4	<i>C. terglouensis</i>	I	3	20	wider	4
4	<i>C. rhaetica</i>	I	3	20+	wider	5
4	<i>C. hokkaidoensis</i>	IX	15-i, j	10	wider	6
4	<i>C. albiflora</i>	III	5-KD	1	narrow A	7
4	<i>C. dioritica</i>	III	5-CT	2	narrow A	8
5	<i>C. lapsanoides</i>	I	2	12	wider	9
5	<i>C. willemetioides</i>	IV	9-AK	2	narrow B	10
5	<i>C. hierosolymitana</i>	III	6	14	wider	11
5	<i>C. montana</i>	II	4-Greece	13	wider	12
5	<i>C. Mungierii</i>	II	4-c, k	7	wider	13
7	<i>C. achyrophoroides</i>	X	18	2	narrow A ?	14
7	<i>C. clymatica</i>	IV	9-KS	2	wider	15
8	<i>C. kilimandscharica</i>	XI	19-KI	5	narrow A	16
8	<i>C. keniensis</i>	XI	19-KE	2	narrow A	17
8	<i>C. suffruticosa</i>	XI	19-ME	1	narrow A	18
8	<i>C. iringensis</i>	XI	19-RM	2	narrow A	19
8	<i>C. meruensis</i>	XI	19-Me, KI	5	narrow B	20
8	<i>C. cameroonica</i>	XI	19-MC	5	narrow A	21
8	<i>C. Schultzii</i>	X	18	3	narrow A ?	22
8	<i>C. urundica</i>	XI	19-UK	1	narrow A	23
8	<i>C. chirindica</i>	XI	19-CH	1	narrow A	24
8	<i>C. congoensis</i>	XI	19-EC	1	narrow A	25
8	<i>C. caudicalis</i>	XI	19-MC ?	2	narrow A	26
8	<i>C. glandulosissima</i>	XI	19-KE +	2	wider	27
8	<i>C. ugandensis</i>	XI	19-FU	1	narrow A	28
8	<i>C. Swynnertonii</i>	XI	19-NY	6	wider	29
8	<i>C. subscaposa</i>	VII	13	6	wider	30
8	<i>C. simulans</i>	XI	19-CH	1	narrow A	31
8	<i>C. Gossweileri</i>	XI	19-CA	1	narrow A	32
8	<i>C. Freisii</i>	XI	19-KU	1	narrow A	33
8	<i>C. Mildbraedii</i>	XI	19-CU	2-3	wider	34
8	<i>C. Bruceae</i>	XI	19-UL	1	narrow A	35
9	<i>C. tingitana</i>	I	1	16	wider	36
9	<i>C. leontodontoides</i>	XII	23	many	wider	37
9	<i>C. subcrostris</i>	XII	24	8	wider	38
10	<i>C. Strausii</i>	IV	9-PS	3	narrow B ?	39
10	<i>C. darvasica</i>	V	10-DA	1	narrow A	40
10	<i>C. songorica</i>	V	10-AT	5	wider ?	41
10	<i>C. sonchifolia</i>	IV	8	2	narrow A ?	42
10	<i>C. ciliata</i>	IV	8	4	wider	43
10	<i>C. latialis</i>	XII	23	13+	wider	44
10	<i>C. bertiscea</i>	II	4	1	narrow A	45
10	<i>C. chondrilloides</i>	II	4	many	wider	46
10	<i>C. bupleurifolia</i>	III	5	3	wider	47
10	<i>C. auriculaefolia</i>	II	4-c	9	wider	48
10	<i>C. Baldaccii</i>	II	4	4	wider	49

TABLE 8
THE ENDEMIC SPECIES OF *CREPIS* OF THE OLD WORLD

Serial number	Phylogenetic group	Altitude class	Moisture class	Duration class	Variability class	Basic chromosome number
1	primitive A	montane	subhumid	perennial	monomorphic	6
2	primitive A	alpine	moist	perennial	monomorphic	6
3	primitive A	alpine	subhumid	perennial	monomorphic	6
4	primitive A	alpine	subhumid	perennial	monomorphic	6
5	primitive A	alpine	subhumid	perennial	monomorphic	—
6	primitive A	alpine	subhumid	perennial	monomorphic	4
7	intermediate	alpine	subhumid?	perennial	monomorphic	4
8	intermediate	alpine	subhumid?	perennial	monomorphic	—
9	primitive A	montane	moist	perennial	monomorphic	6
10	primitive B	low?	arid?	perennial	monomorphic	6
11	intermediate	low	arid	perennial	monomorphic	6
12	intermediate	low	arid	perennial	polymorphic	6
13	intermediate	montane	arid	perennial	polymorphic	6
14	primitive B	montane	subhumid	perennial	monomorphic	—
15	intermediate	montane	arid?	perennial	monomorphic	—
16	primitive A	montane	moist	perennial	monomorphic	4
17	primitive A	montane	moist	perennial	monomorphic	—
18	primitive A	alpine	subhumid	perennial	monomorphic	4
19	primitive A	montane	subhumid	perennial	monomorphic	—
20	primitive A	montane	subhumid	perennial	polymorphic	—
21	primitive A	montane	subhumid	perennial	monomorphic	—
22	primitive B	montane	moist	perennial	monomorphic	—
23	primitive B	montane	moist	perennial	monomorphic	—
24	intermediate	montane	subhumid	perennial	monomorphic	—
25	intermediate	low	subhumid	perennial	monomorphic	—
26	intermediate	low	subhumid	perennial	monomorphic	—
27	intermediate	montane	subhumid	perennial	monomorphic	—
28	intermediate	low	subhumid	perennial	monomorphic	—
29	intermediate	low	subhumid	perennial	polymorphic	—
30	intermediate	montane	moist	perennial	monomorphic	—
31	intermediate	montane	subhumid	perennial	monomorphic	—
32	intermediate	low	moist	perennial	monomorphic	—
33	intermediate	montane	subhumid	perennial	monomorphic	—
34	intermediate	low	subhumid	perennial	monomorphic	—
35	intermediate	montane	subhumid	perennial	monomorphic	—
36	primitive B	low	arid	perennial	polymorphic	5
37	intermediate	low	arid	perennial	polymorphic	5
38	advanced	low	arid	annual	polymorphic	5
39	primitive B	montane	subhumid?	perennial	monomorphic	—
40	primitive B	montane	subhumid	perennial	monomorphic	—
41	primitive B	montane	subhumid	perennial	monomorphic	—
42	primitive B	low	subhumid	perennial	monomorphic	—
43	primitive B	low	subhumid	perennial	monomorphic	5
44	intermediate	low	subhumid	perennial	polymorphic	4
45	intermediate	montane	arid?	perennial	monomorphic	—
46	intermediate	low	subhumid	perennial	monomorphic	4
47	intermediate	montane	subhumid	perennial	polymorphic	—
48	primitive B	montane	arid	perennial	monomorphic	—
49	primitive B	montane	subhumid	perennial	monomorphic	5

TABLE 8—(Continued)

Section	Species	Region	Area	Number of localities known	Distribution class	Serial number
10	<i>C. turcica</i> ...	II	4	4	narrow B	50
10	<i>C. Pantocsekii</i> ...	II	4	6	wider	51
10	<i>C. Triasii</i> ...	I	1-a	many	narrow B	52
10	<i>C. Raulini</i> ...	II	4-c	3	narrow B	53
10	<i>C. albanica</i> ...	II	4-NA	2	narrow A	54
10	<i>C. macropus</i> ...	III	5	8	wider	55
10	<i>C. oporinoides</i> ...	I	1	18	wider	56
10	<i>C. dens-leonis</i> ...	IV	8-CA	1 or 2	narrow A ?	57
10	<i>C. Sibthorpiana</i> ...	II	4-c	2	narrow B	58
10	<i>C. khorassanica</i> ...	IV	9-KN	1	narrow A	59
10	<i>C. incana</i> ...	II	4	5	wider	60
10	<i>C. taygetica</i> ...	II	4-TA	1	narrow A	61
10	<i>C. turcomanica</i> ...	IV	9-AC	2	narrow A ?	62
10	<i>C. Guioliania</i> ...	II	4-MS	1	narrow A	63
10	<i>C. crocifolia</i> ...	II	4-TA	1	narrow A	64
10	<i>C. athoa</i> ...	II	4-AO	1	narrow A	65
11	<i>C. Schachtii</i> ...	II	4-AB	1	narrow A	66
11	<i>C. pinnatifida</i> ...	III	5	3-5	wider	67
11	<i>C. oreades</i> ...	V	10-UT, P-A	12+	wider	68
11	<i>C. tenerima</i> ...	X	18-SM	1	narrow A	69
11	<i>C. xylorrhiza</i> ...	X	18-SM	2	narrow A	70
11	<i>C. Hookeriana</i> ...	I	1-GA	7	wider	71
11	<i>C. Faureliana</i> ...	I	1-SA	1	narrow A	72
11	<i>C. Robertioides</i> ...	III	6-LI, AL	17	narrow B	73
11	<i>C. heterotricha</i> ...	IV	9	5	wider	74
11	<i>C. armena</i> ...	III	5	5	wider	75
11	<i>C. demavendi</i> ...	IV	9-EL	1	narrow A	76
11	<i>C. abyssinica</i> ...	X	18	2	narrow A ?	77
12	<i>C. corniculata</i> ...	V	10-P, AI, TI	7	wider	78
12	<i>C. alaica</i> ...	V	10-AI, TI	4	narrow B	79
12	<i>C. naniforma</i> ...	VI	11-HI	3	wider	80
12	<i>C. lactea</i> ...	V	10-P, TS	6	wider	81
13	<i>C. gymnopus</i> ...	IX	15-i	4	wider	82
16	<i>C. connexa</i> ...	IV	9-SV	2	narrow B ?	83
16	<i>C. sahendi</i> ...	IV	8	6	wider	84
16	<i>C. purpurea</i> ...	III	7	3	narrow B	85
16	<i>C. elbrusensis</i> ...	IV	9-EL	3	narrow B	86
16	<i>C. frigida</i> ...	III	5	4	wider	87
17	<i>C. napifera</i> ...	VII	13	12	wider	88
18	<i>C. Phoenix</i> ...	VII	13	5+	wider	89
18	<i>C. Bodinieri</i> ...	VII	13	10	wider	90
18	<i>C. rigescens</i> ...	VII	13	17	wider	91
18	<i>C. lignea</i> ...	VII	13	14	wider	92
18	<i>C. chloroclada</i> ...	VII	13-SH	1	narrow A	93
19	<i>C. palaestina</i> ...	III	6	10	wider	94
19	<i>C. amanica</i> ...	III	6-DU	1	narrow A	95
19	<i>C. Stojanovi</i> ...	II	4	4	narrow B	96
19	<i>C. pterothecoides</i> ...	III	6-AL, etc.	4	narrow B	97
20	<i>C. syriaca</i> ...	III	6	13	wider	98

TABLE 8—(Continued)

Serial number	Phylogenetic group	Altitude class	Moisture class	Duration class	Variability class	Basic chromosome number
50	intermediate	montane	subhumid	perennial	polymorphic	—
51	intermediate	montane	subhumid	perennial	monomorphic	—
52	intermediate	low	arid	perennial	monomorphic	4
53	intermediate	alpine	subhumid	perennial	monomorphic	5
54	intermediate	montane	subhumid	perennial	monomorphic	—
55	intermediate	low	arid	perennial	monomorphic	—
56	intermediate	montane	subhumid	perennial	polymorphic	4
57	intermediate	montane	subhumid?	perennial	monomorphic	—
58	intermediate	alpine	subhumid	perennial	monomorphic	—
59	intermediate	alpine	subhumid	perennial	monomorphic	—
60	intermediate	montane	subhumid	perennial	monomorphic	4
61	intermediate	alpine	subhumid	perennial	monomorphic	5
62	intermediate	montane	subhumid	perennial	monomorphic	—
63	intermediate	montane	subhumid?	perennial	monomorphic	—
64	intermediate	alpine	subhumid	perennial	monomorphic	—
65	intermediate	alpine	subhumid	perennial	monomorphic	—
66	primitive B	montane	arid	perennial	monomorphic	5
67	intermediate	alpine	subhumid	perennial	monomorphic	—
68	primitive B	montane	arid	perennial	polymorphic	4
69	intermediate	montane	moist	perennial	monomorphic	—
70	intermediate	alpine	moist	perennial	monomorphic	—
71	primitive B	alpine	subhumid	perennial	monomorphic	4
72	intermediate	montane	arid	perennial	monomorphic	—
73	intermediate	alpine	moist	perennial	monomorphic	4
74	intermediate	alpine	subhumid	perennial	polymorphic	—
75	intermediate	alpine	subhumid	perennial	polymorphic	—
76	intermediate	alpine	moist?	perennial	monomorphic	—
77	intermediate	alpine	arid?	perennial	monomorphic	—
78	intermediate	alpine	moist?	perennial	monomorphic	—
79	intermediate	alpine	moist	perennial	monomorphic	—
80	intermediate	alpine	moist	perennial	monomorphic	—
81	intermediate	alpine	moist	perennial	monomorphic	—
82	intermediate	alpine	moist?	perennial	monomorphic	4
83	primitive B	montane	subhumid	perennial	monomorphic	—
84	intermediate	alpine	subhumid	perennial	monomorphic	—
85	intermediate	low	subhumid	perennial	monomorphic	—
86	intermediate	alpine	subhumid	perennial	monomorphic	—
87	intermediate	alpine	subhumid	perennial	monomorphic	—
88	intermediate	montane	subhumid	perennial	monomorphic	—
89	intermediate	montane	subhumid	perennial	polymorphic	—
90	intermediate	montane	subhumid?	perennial	polymorphic	—
91	intermediate	montane	arid?	perennial	polymorphic	—
92	intermediate	montane	arid	perennial	polymorphic	—
93	intermediate	montane	arid	perennial	monomorphic	—
94	advanced	low	subhumid	annual	polymorphic	4
95	advanced	montane	subhumid?	annual	monomorphic	—
96	advanced	low	arid	annual	monomorphic	4
97	advanced	montane	arid	annual	polymorphic	4
98	advanced	low	arid	annual	polymorphic	5 (+)

TABLE 8—(Concluded)

Section	Species	Region	Area	Number of localities known	Distribution class	Serial number
20	<i>C. Schimperi</i>	X	18	6	wider	99
20	<i>C. eritreensis</i>	X	17	5	narrow A	100
20	<i>C. Thomsonii</i>	VI	12	16	wider	101
20	<i>C. tybakiensis</i>	II	4-c	1	narrow A	102
21	<i>C. tibetica</i>	VII	13	5	wider	103
21	<i>C. Gmelini</i>	VIII	14	2	wider	104
21	<i>C. elongata</i>	VII	13	4	wider	105
23	<i>C. patula</i>	XII	22	7	wider	106
23	<i>C. Dioscoridis</i>	II	4-Greece	many	wider	107
23	<i>C. multiflora</i>	II	4-Aegean	20+	wider	108
24	<i>C. insignis</i>	III	6	1	narrow A	109
24	<i>C. corymbosa</i>	XII	23-Italy, h	8	wider	110
24	<i>C. fuliginosa</i>	II	4-Greece	many	wider	111
24	<i>C. cretica</i>	II	4-c	many	wider	112
24	<i>C. apula</i>	XII	23-Italy	3	wider	113
24	<i>C. Suffreniana</i>	XII	23-France	10	wider	114
25	<i>C. spathulata</i>	XII	23-b	10?	wider	115
25	<i>C. Salzmannii</i>	XII	24	5	wider	116
25	<i>C. Fontiana</i>	XII	24	2	narrow B	117
25	<i>C. Bourgeau</i>	XII	24	4	narrow B?	118
25	<i>C. canariensis</i>	XII	25-g	many	narrow B	119
25	<i>C. divaricata</i>	XII	25-e	1	narrow A	120
25	<i>C. Noronhaca</i>	XII	25-f	6	narrow A	121
25	<i>C. Balliana</i>	XII	24	1	narrow A	122
25	<i>C. libyca</i>	XII	20	9	wider	123
25	<i>C. Claryi</i>	XII	24-SA	2	narrow A	124
26	<i>C. juvenalis</i>	XII	21	6	wider	125
26	<i>C. aculeata</i>	III	6	9	wider	126
26	<i>C. atheniensis</i>	II	4-Greece	1	narrow A	127
26	<i>C. aspera</i>	III	6	19	wider	128
26	<i>C. Muhlisii</i>	III	5	2	narrow A	129
27	<i>C. Forskalii</i>	X	16	2	narrow A	130
27	<i>C. bellidifolia</i>	XII	24-a, d	many	wider	131
27	<i>C. bursifolia</i>	XII	24-Italy, b	12	wider	132
27	<i>C. filiformis</i>	XII	20	2	narrow A?	133

TABLE 8—(Concluded)

Serial number	Phylogenetic group	Altitude class	Moisture class	Duration class	Variability class	Basic chromosome number
99	advanced	montane	arid	annual	monomorphic	—
100	advanced	montane	subhumid	annual	monomorphic	5
101	advanced	montane	arid?	annual	polymorphic	5
102	advanced	low	arid	annual	monomorphic	—
103	intermediate	alpine	subhumid?	perennial	polymorphic	—
104	intermediate	montane	subhumid	perennial	monomorphic	—
105	intermediate	montane	subhumid	perennial	monomorphic	—
106	intermediate	low	moist	perennial	monomorphic	4
107	advanced	low	arid	annual	polymorphic	4
108	advanced	low	arid	annual	polymorphic	4
109	advanced	low	arid	annual	monomorphic	—
110	advanced	low	arid	annual	polymorphic	4
111	advanced	montane	arid	annual	polymorphic	3
112	advanced	montane	arid	annual	monomorphic	4
113	advanced	low	arid	annual	monomorphic	4
114	advanced	low	arid	annual	monomorphic	4
115	intermediate	low?	arid	perennial	monomorphic	—
116	intermediate	low	arid	perennial	monomorphic	—
117	intermediate	low	subhumid	perennial	monomorphic	4
118	intermediate	low	subhumid	perennial	monomorphic	4
119	intermediate	low	arid	perennial	monomorphic	4
120	intermediate	low	subhumid	perennial	monomorphic	4
121	intermediate	low	arid	perennial	monomorphic	4
122	intermediate	low	subhumid	perennial?	monomorphic	—
123	advanced	low	arid	perennial	monomorphic	4
124	advanced	montane	arid	annual	monomorphic	—
125	advanced	low	arid	annual	polymorphic	4
126	advanced	low	arid	annual	monomorphic	4
127	advanced	low	arid	annual	monomorphic	—
128	advanced	low	arid	annual	polymorphic	4
129	advanced	low	arid	annual	monomorphic	—
130	advanced	montane	subhumid	perennial	monomorphic	—
131	advanced	montane	subhumid	perennial	polymorphic	4
132	advanced	low	subhumid	perennial	monomorphic	4
133	advanced	low	arid	annual	monomorphic	—

TABLE 9
ENDEMIC REGIONS AND AREAS FOR OLD WORLD CREPIS

<i>Regions</i>	<i>Areas</i>
I. Southwestern Europe; Alps; northwestern Morocco.....	1. S. Spain and N. W. Morocco 2. N. E. Spain and W. France 3. European Alps
II. Balkan Peninsula.....	4. Balkan Peninsula
III. Asia Minor; Syria-Palestine; Crimea.....	5. Asia Minor 6. Syria and Palestine 7. Crimea
IV. Caucasus; Iran.....	8. Caucasus region 9. Iran
V. Turkestan-Pamir-Altai region.....	10. Turkestan, i.e., E. and N. Russian Turkestan and the Pamir-Altai Mountains
VI. Northwestern India.....	11. N. W. Himalaya Mountains, high alpine 12. N. W. India-Baluchistan, low montane
VII. Southeastern Asia.....	13. S. E. Asia (= S. E. Tibet, S. W. China, N. Burma, Laos, Annam)
VIII. Eastern Siberia	14. E. Siberia (Okhotsk district)
IX. Northern Japan.....	15. Hokkaido-Sakhalin
X. Abyssinia; Eritrea; southwestern Arabia	16. S. W. Arabia (in Yemen Province) 17. Eritrea 18. N. Abyssinia, mountains
XI. Africa, tropical.....	19. Africa, tropical (isolated localities)
XII. Lybia-Morocco-Cadiz (littoral); southern and western maritime Italy and southern France; Madeira and Canary Islands.....	20. Lybia (littoral) 21. Tunisia (middle and southern) 22. E. Algeria (littoral) 23. S. Italy and Toscana, Sicily, Sardinia, Corsica; S. France 24. W. Algeria, N. Morocco, Cadiz (mostly littoral) 25. Madeira and Canary Islands

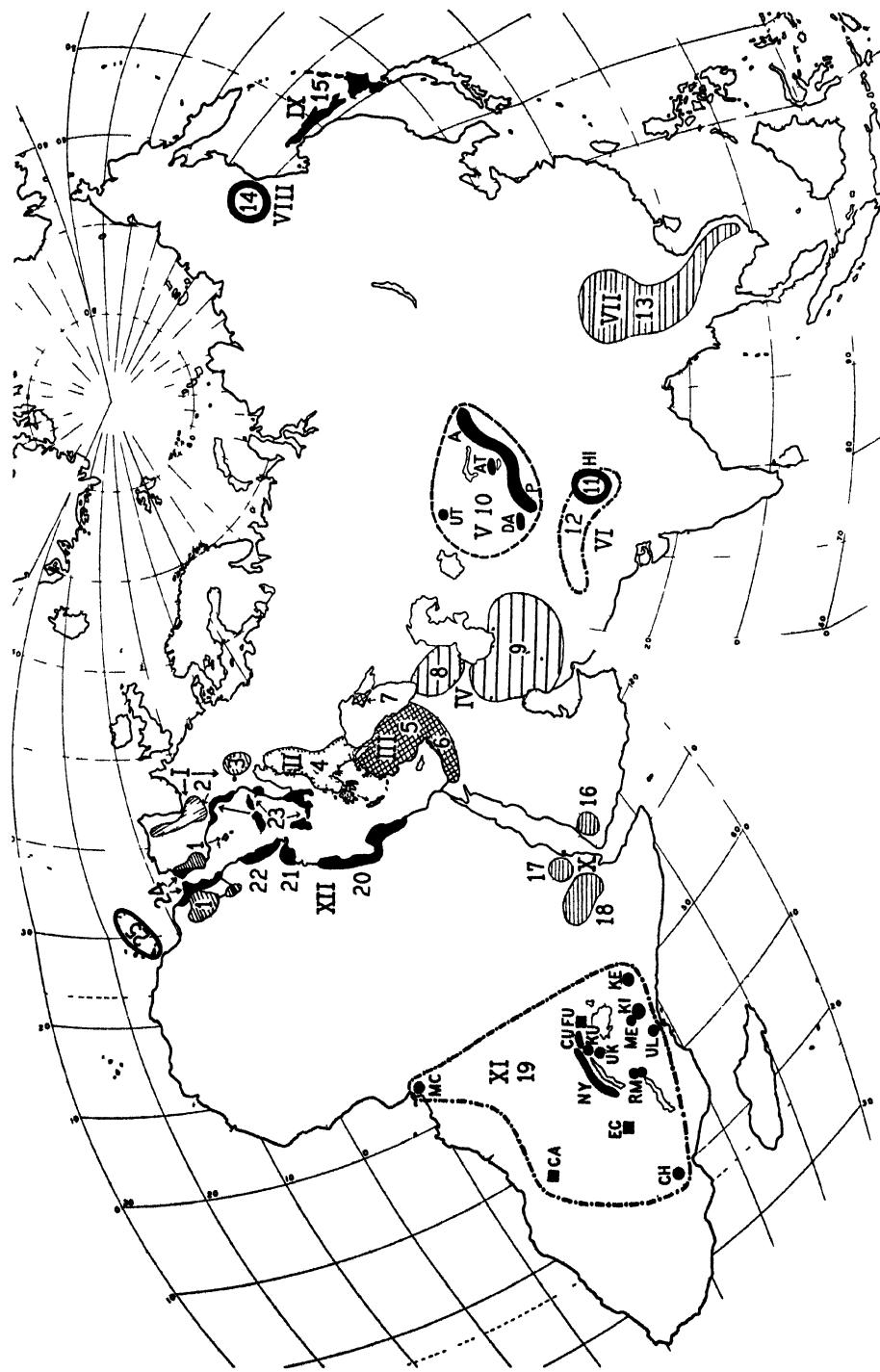


Fig. 10. Map of the Old World, showing the location and approximate size of all the endemic regions (indicated by Roman numerals) and areas (Arabic numerals) for *Crepis*. See tables 8 and 9. Based on Goode Base Map No. 201 PC. By permission of the University of Chicago Press.

things to catch the attention. It should be emphasized that all of the eighteen endemic species found in this area are extremely local in distribution. All but three, from the data now available, occur on only one or two mountains or in a single mountain range. These mountains and ranges are shown as solid circles or narrow ellipses. The other three species, shown as solid squares, are known from single stations which are at low elevation. The key to the symbols used to designate endemic localities in table 8, some of which symbols are also used in areas 10 and 19 in figure 10, are as follows:

INDIVIDUAL MOUNTAINS OR RANGES OF MOUNTAINS

- AB. Mt. Ali Botusch, eastern Macedonia, Bulgaria.
- AC. Achal-Tekko Mts., southwestern Turkestan (area 9, region IV).
- AI. Alai Mts., Ferghana, eastern Russian Turkestan.
- AK. Alla-Dagh and Kopet-Dagh, northeastern Iran.
- AL. Anti-Liban Mts., southwestern Syria.
- AO. Mt. Athos, Hagiion Oros Peninsula, Greece.
- AT. Ala-Tau Mts., Central Asia.
- CA. Caucasus Mts.
- CH. Mt. Chirinda, southeastern Africa.
- CT. Cilician Taurus, southern Asia Minor.
- DA. Darvas Mts., eastern Russian Turkestan.
- DU. Mt. Dümanly, Amanus Mts., northern Syria.
- CU. Congo-Uganda plateau north of Lake Kiwu, tropical Africa.
- EL. Elburz Mts., northern Iran.
- GA. Great Atlas Mts., Morocco.
- HI. Himalaya Mts., Kashmir, high alpine.
- KD. Kop-Dagh, western Armenia.
- KE. Mt. Kenya, eastern tropical Africa.
- KI. Mt. Kilimanjaro, eastern tropical Africa.
- KN. Kuh-i-Nishapur Mts., northeastern Iran.
- KS. Kuh-i-Gerru and Schuturun Mts., western Iran.
- KU. Mountains south of Lake Kiwu, tropical Africa.
- LI. Liban Mts., southwestern Syria.
- MC. Mt. Cameroon, western tropical Africa.
- ME. Mt. Meru, eastern tropical Africa.
- MS. Mt. Smolika, western Greece.
- NA. North Albanian Alps.
- NY. Mountains of Nyasaland, extending into Belgian Congo, Africa.
- P. Pamir Mts., southern Central Asia.
- P-A. Pamir-Altai mountain system.
- PS. Kuh-i-Parrau and Mt. Shahu, western Iran.
- RM. Mt. Rungwe and Mt. Mbeya, tropical Africa.
- SA. Saharan Atlas, southern Algeria.
- SH. Shan Hills, eastern Burma.
- SM. Simen Mts., Amhara-Tigre Province, Abyssinia.
- SV. Shahu and Avroman Mts., western Iran.
- TA. Mt. Hagios Elias, Taygetos Mts., southwestern Greece.
- TL. Transalai Mts., Ferghana, eastern Russian Turkestan.
- TS. Tien Shan Mts., Central Asia.
- UK. Urundi Province, Kisozi, tropical Africa.
- UL. Uluguru Mts., Tanganyika Province, tropical Africa.
- UT. Ulu-Tau Mts., northern Russian Turkestan.

SINGLE LOWLAND STATIONS IN AFRICA

(Shown as solid squares in figure 10.)

- CA. Cului, Angola.
- EC. Elisabethville, southeastern Belgian Congo.
- FU. Fort Portal, Uganda.

INDIVIDUAL ISLANDS OR GROUPS OF ISLANDS

- a. Balearic (Majorca).
- b. Sicily.
- c. Crete.
- d. Corsica-Sardinia.
- e. Madcira.
- f. Porto Santo.
- g. Lanzarote, Fuerteventura.
- h. Corfu-Cephalonia.
- i. Hokkaido (or Yezo).
- j. Sakhalin.
- k. Karpathos.

The distribution of the twelve endemic regions defines the east-west distribution of the genus as a whole almost completely, the gaps between the endemic regions being occupied more or less by the various widespread species. In this connection it should be repeated that the total evidence on geographic distribution in *Crepis*, considered in relation to the evidence on phylogeny, definitely indicates that the center of origin and early development of *Crepis* was in Central Asia, in the Altai-Tien Shan mountain region in the northeastern part of region V (fig. 10); and that the present wide distribution of the genus was accomplished through migration from that center. One migration trend was to the east and northeast, resulting in the two endemics of Japan and the one in the Okhotsk district of Siberia (regions VIII and IX, fig. 10). Another trend was to the southeast, resulting in the nine endemic species found in region VII. Most important of all the migration trends from Central Asia, in terms of the number of species involved, was the southwesterly trend across Turkestan and Iran. From this region three branches led to northwestern and tropical Africa, to the Caucasus, Asia Minor, and southern Europe, and to the eastern Mediterranean and north African littoral. The point to be emphasized here is that the distribution of the endemic regions for *Crepis* is entirely consistent with the history of the genus as a whole.

PHYLOGENY AND ENDEMISM IN CREPIS

Based on the evidence from comparative morphology and cytogenetics, it has been possible to classify all the species of *Crepis* on a relative phylogenetic basis with some degree of assurance. For purposes of the present discussion they have been grouped into three classes, the more primitive, the intermediate, and the more advanced species. In table 10 are shown the relations of the endemic species in these phylogenetic groups to the size of area occupied by each species, to its altitude and moisture classification, and to its life-duration and variability.

Considering first the totals in the right-hand column, it will be noted that 29 of the endemic species are primitive and 29 are advanced, whereas 75, or more than one-half of them, are intermediate. The fact that *Crepis* may evidently be described as a conservative genus becomes more patent when it is realized that of the 29 advanced endemics only some half-dozen desert or montane annuals can be considered as very highly specialized species. Apparently no correlation exists between the phylogenetic grouping and extent of distribution (narrow *vs.* wider), since about one-third of all the endemics are narrow and two-thirds are wider, and these same proportions hold roughly for each of the three phylogenetic classes. In altitudinal distribution there is positive correlation between primitive type and alpine altitude and very strong positive correlation between advanced type and low altitude. In the moisture classes we find that, of the 104 endemics in the primitive and intermediate groups taken together, just one-fifth occur under arid conditions,

TABLE 10
RELATIONS BETWEEN THE PHYLOGENETIC GROUPS OF 133 ENDEMIC SPECIES OF CREPIS AND THEIR EXTENT OF NATURAL DISTRIBUTION, ELEVATION, GENERAL
MOISTURE CONDITION, DURATION OF LIFE, AND VARIABILITY

Phylogenetic groups	Distribution classes		Altitude classes				Moisture classes			Duration classes			Variability classes		Totals
	Narrow	Wider	Alpine	Montane	Low	Moist	Subhumid	Arid	Perennial	Annual or biennial	Monomorphic	Poly-morphic			
Primitive.....	11	18	7	18	4	6	18	5	29		26	3		29	
Intermediate.....	28	47	24	28	23	12	46	17	75		61	14		75	
Advanced.....	9	20		10	19		6	23	4	25	17	12		29	
Totals	48	85	31	56	46	18	70	45	108	25	104	29	133		

TABLE 11
RELATIONS OF THE HAPLOID CHROMOSOME NUMBERS 6, 5, 4, 3 TO THE PHYLOGENETIC GROUP, EXTENT OF NATURAL DISTRIBUTION, ELEVATION, MOISTURE,
DURATION OF LIFE, AND VARIABILITY OF 52 ENDEMIC SPECIES OF CREPIS
(The polyploid endemics *C. ciliata*, *C. inacma*, and *C. tagetica* are omitted)

Chromosome numbers	Phylogenetic groups			Distribution classes			Altitude classes			Moisture classes			Duration classes			Variability classes		Totals
	Primitive	Intermediate	Advanced	Narrow	Wider	Alpine	Montane	Low	Moist	Sub-humid	Arid	Perennial	Annual or biennial	Monomorphic	Poly-morphic			
<i>n</i> = 6.....	6	3			9	3	3	2	3	4	9		7	2	9			
<i>n</i> = 5.....	3	2	4	2	7	1	4	4		3	6	5	4	4	5	9		
<i>n</i> = 4.....	5	13	15	6	27	6	4	23	5	14	14	21	12	22	11	33		
<i>n</i> = 3.....				1	1		1			1		1		1	1	1	1	
Totals	14	18	20	8	44	10	12	30	7	20	25	35	17	33	19	52		

whereas four-fifths of the advanced endemics occur under arid conditions. Hence, there is strong positive correlation between advanced type and arid environment. In the life-duration classes the differences are most striking—all the primitive and intermediate endemics are perennial, whereas nearly all of the advanced endemics are either annual or biennial, most of them being annual. In variability, a stronger tendency exists toward polymorphism in the advanced than in the intermediate or primitive endemics. *All of the primitive and intermediate endemics are perennial species, more than four-fifths of them being monomorphic and occurring at montane or alpine elevations and under subhumid or moist conditions. Most of the advanced endemics are annual species, two-fifths of them being polymorphic; none occurs at alpine elevations and about three-fourths of them are found at low elevations and under arid conditions.*

It may be inferred that the advanced, annual endemic species which are polymorphic are mostly of wider distribution and occur at low altitude, under arid conditions. This inference has been verified by reexamination of the original data. There are twenty-five annual endemic species (table 10) of which twenty-three occur in an arid climate and all but one of these at low altitude. Only eighteen are known to have a wider distribution; but, of the other seven, six are known as yet only from the type locality and further collections may show that some of these also have a wider distribution.

The contrast between this group of advanced endemics and the strictly alpine endemics is very striking. Of the thirty-one alpine endemics, all are perennial; twenty-nine are monomorphic, and only two are polymorphic; and all but one occur under subhumid or moist conditions. Six of them are primitive and twenty-five are intermediate, there being no advanced alpine species. *This means, of course, that the alpine endemics are all relatively old species and adapted to mesophytic conditions; whereas the lowland endemics of advanced type are relatively young species and adapted to xerophytic conditions.*

But the contrast between the two groups does not hold for size of distributional area. Of the thirty-one alpine endemics, twenty-one are wider and only ten are narrow in distribution. Furthermore, there are ten other alpine species of *Crepis* which are so extensive in geographic distribution that they are not considered to be endemic. For example, *C. conyzæfolia* is a primitive alpine-subalpine species distributed from the Pyrenees to the Balkan Peninsula and in northern Asia Minor, Transcaucasia, northern Persia, and the Altai region. Such evidence, together with the prevalence of wide distribution among the alpine endemics, certainly indicates that the alpine endemics were formerly more widely distributed and have become restricted to their present locations presumably through radical changes in the environment. In other words, the alpine endemics are *relic species* in the usual meaning of that term (see definition of Wulff, in Komarov, 1941, p. 57).

The evidence on chromosome numbers is in good agreement with the foregoing generalizations. In table 11 fifty-two diploid endemic species are classified opposite their numbers 6, 5, 4, or 3 and in relation to phylogenetic grouping and the other classifications used in table 10. Phylogenetically, the 6-paired endemics are all primitive or intermediate, none is advanced; whereas the 5-paired endemics are about evenly divided among the three groups and the 4-paired endemics are mostly intermediate or advanced. The one 3-paired endemic, *C. fuliginosa*, is advanced, widely distributed, montane, xerophytic, annual, and polymorphic. In distribution, all of the 6-paired endemics as well as most of the 5's and 4's are wider; but the small number of narrow endemics that have been examined cytologically may be partly due to difficulties in obtaining them in living condition. The data on alti-

TABLE 12
RELATIONS BETWEEN THE ENDEMIC REGIONS FOR CREPIS AND THE PHYLOGENETIC GROUP, ALTITUDE, AND DURATION OF LIFE OF 133 ENDEMIC SPECIES—
AND THE DIPLOID CHROMOSOME NUMBERS OF 52 OF THE SAME SPECIES

Endemic regions	Phylogenetic groups						Altitude classes			Duration classes			Diploid chromosome numbers		
	Totals		Primitive A	Intermediate B	Alpine	Mon- tanous	Low	Peren- nial	Annual or bi- ennial	6	5	4	3	Totals	
I. S. W. Europe; Alps; N. W. Morocco (mountains).....	8	3	2	3	3	3	2	8		2	1	3		6	
II. Balkan Peninsula.....	26	2	3	14	7	6	13	7	19	7	4	3	6	1	14
III. Asia Minor; Syria-Palestine; Crimea.....	18			10	8	6	3	9	10	8	1	1	6		8
IV. Caucasus; Iran.....	13			5	8		5	5	3	13		1			1
V. Turkestan-Pamir-Altai region.....	6			3	3		3	3	6			1			1
VI. N. W. India.....	3	1	1	1	2		1		2	1	1	1			2
VII. S. E. Asia.....	9			9	1	8		9							
VIII. E. Siberia.....	1			1		1		1							
IX. N. Japan.....	2	1		1		2			2			2			2
X. Abyssinia; Eritrea; S. W. Arabia.....	8		2	3	3	2	6		6	2		1			1
XI. Africa (tropical).....	18	6	1	11	1	11		6	18			2			2
XII. Libya to Morocco (littoral); Madeira and Canary Islands; S. Italy; S. France.	21			11	10		2	19	14	7		2	13		15
Totals	133	13	16	75	29	31	56	46	108	25	9	9	33	1	52

tudinal distribution indicate no correlations except in the 4-paired species, which are mostly of low elevation. As for moisture relations, most of the fifty-three species are about equally divided between subhumid and arid and this holds for each of the chromosome number classes. Under duration of life we find that all of the 6-paired endemics are perennial, whereas about one-third of both 5's and 4's are annual. Obviously, reduction in length of life has gone along with reduction in the number of chromosomes. As for variability, there is little difference between the chromosome number classes in the proportion of monomorphic and polymorphic species. The most significant facts derived from this analysis are: (1) *The 6-paired species are mostly primitive and all perennial, but they are about equally distributed among the altitude and moisture classes.* (2) *The 4-paired species are mostly intermediate or advanced and of low elevation, but they are about equally divided between mesophytic and xerophytic environments.* (3) *These facts seem to indicate that adaptation from mesophytic to xerophytic conditions has been going on in this genus over a very long period of time.*

THE DISTRIBUTION AND PHYLOGENY OF *CREPIS* ENDEMICS

In table 12 each of the endemic *Crepis* species is tabulated according to the endemic region in which it occurs and its phyletic, altitude, and life-duration class; also, the fifty-three endemics that have had their chromosomes counted are tabulated according to chromosome number as well as the region where they occur.

Considering first the primitive endemics, it will be noted that two grades, A and B, are recognized. The thirteen species in the A group are definitely more primitive, on morphological grounds, than those of the B group. Eleven of these most primitive endemics are either alpine or montane and are restricted to southwestern Europe or the Balkan Peninsula or to a few high mountains in tropical Africa. The other two are alpine species, one in the western Himalaya Mountains and the other in the northern islands of Japan. Thus, the most primitive *Crepis* endemics are now mostly distributed at great distances from the assumed center of origin for the genus. Since most of the advanced endemics are closer to Central Asia than to southwestern Europe, the distribution of the most primitive and most advanced endemics in *Crepis* conforms in general with Matthew's principle of radial distribution of older types from a common center accompanied by the development of more advanced types nearer the center (Matthew, 1915). This conformity with Matthew's principle, as was pointed out in the preceding chapter, is also apparent from the distribution of all the species (including the endemics) in several of the more primitive sections of *Crepis*. These facts provide a sound basis for the hypothetical history of *Crepis*, which starts with the origin and early development of the genus in Central Asia.

Considering next the totals for the twelve regions (table 12, column 2), it is clear that the greatest concentrations of endemics exist in the Balkan Peninsula, in Asia Minor and adjacent areas, in tropical Africa, and in the Mediterranean littoral. But these four regions differ with respect to the phylogenetic status of their endemics. In the Balkan Peninsula about one-half of the endemics are intermediate, whereas one-fourth are primitive (A + B) and one-fourth are advanced. These twenty-six species are similarly divided between montane, alpine, and low elevations; the seven advanced species are all annuals. Evidently, the highly diversified conditions in that region have favored the persistence of both primitive and intermediate endemics as well as the development of advanced endemics. In Asia Minor and the Mediterranean littoral, however, the endemics are all either intermediate or advanced. But the fact that there are no primitive endemics in Asia Minor is

probably due to the generally more arid climate of that region as compared with the Balkan Peninsula as a whole. In tropical Africa, on the other hand, we find just the opposite situation. The eighteen endemics are all either intermediate or primitive; and this is also true of four other tropical African species which are so

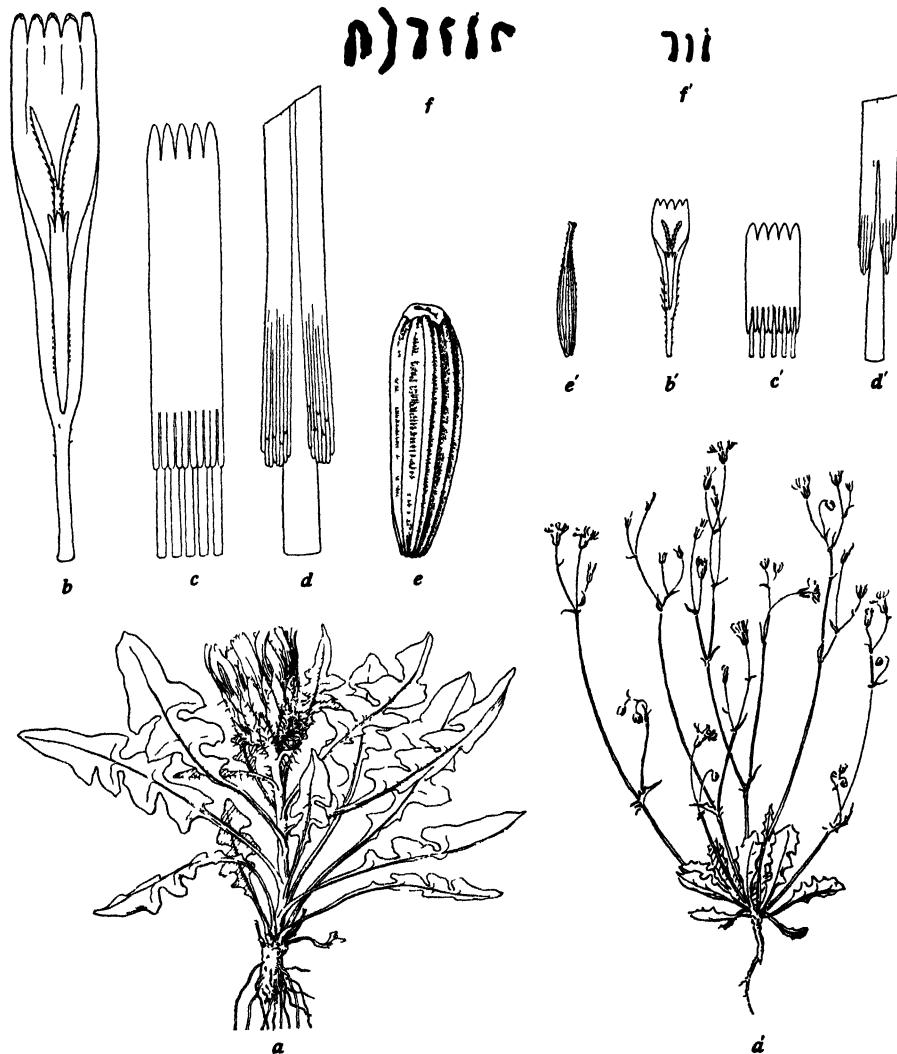


Fig. D. *a-f*, *Crepis terglouensis*: *a*, plant, $\times \frac{1}{2}$; *b*, floret lacking the ovary, $\times 3$; *c*, anther tube slit and opened out, $\times 6$; *d*, detail of anther appendages, $\times 24$; *e*, achene, $\times 6$; *f*, haploid set of chromosomes, $\times 925$. *a'-f'*, *Crepis fuliginosa*: all as above.

widely distributed that they are not included here as endemics. This absence of advanced species in tropical Africa probably indicates that the more uniform and favorable conditions of that region have favored the persistence of more primitive types without inducing the development of very advanced types.

Compared with the four regions that are richest in endemics, the following regions have only one-third to one-half as many in each region: southwestern Europe, the Caucasus-Iran region, Abyssinia and adjacent small areas, and southeastern Asia.

One of these, the Abyssinian region, differs from the other four in having all the phyletic groups represented. The ten endemics of this region are all montane except the two primitive species, which are alpine; and, yet, four of these montane species are advanced. It will be recalled, however, that certain other advanced species are montane. This is true of the one 3-paired endemic, *C. fuliginosa*, which occurs in southern Greece, and of its 4-paired close relative, *C. cretica*. The three other regions contain only perennial endemics, none of which is advanced, some being intermediate and some primitive. Southwestern Europe and tropical Africa are important regions for the most primitive endemics, since nine of the twenty-six endemics found in those two regions are classed as primitive-A. Thus, at the western extremes of distribution for *Crepis*, we find the greatest concentration of the most primitive endemics in the genus.

In order to give another picture of the morphological contrasts between the most primitive and the most advanced species in the genus, *C. terglouensis*, an alpine endemic of the European Alps, is shown in fig. D, *a*–*f*, and *C. fuliginosa*, a lower montane endemic of Greece, in fig. D, *a'*–*f'*. The plants and their parts are drawn at comparable scales. It will be noted, also, that in their haploid sets of chromosomes, the two species represent the extremes of karyotype variation found in this genus.

With reference to the chromosomes of fifty-two of the endemic species (table 12), it is clear that the 6-paired endemics, except for one species, *C. kashmirica*, of northwestern India, are restricted to regions I to IV. In fact, two-thirds of them occur in the mountains of southwestern Europe and the Balkan Peninsula. But the 5-paired endemics are widely distributed, and the 4-paired species still more widely, with a strong representation in the Mediterranean littoral. The distribution of chromosome numbers among the endemic regions is consistent with the morphological evidence in showing that the oldest endemics are mostly in the mountains of southern Europe, whereas the youngest endemics are mostly in the Mediterranean littoral and closely adjacent areas. This evidence supports the general hypothesis, based on morphology and geographic distribution in the genus as a whole, concerning the origin and distribution of the genus. Chromosome number is considered here merely as one criterion of phylogenetic relations and not with reference to the genetic processes which made evolution possible (see next chapter, pp. 145–147).

It should be mentioned here, however, that the many changes in topography and the gradually increasing desiccation of the climate in southwestern Asia and the Mediterranean region must have been important causes of speciation. In *Crepis* the endemic areas most affected by these changing conditions are 1–9 and 21–24 (see fig. 10), where more than 60 per cent of the endemic species exist today.

The nature of the substratum is another environmental factor which may have had an important influence on the history of *Crepis*. The available data on the more primitive species are too scanty to permit an analysis; but the information at hand provides the following observations which may be significant. Although the most primitive endemic, *C. geracioides*, of the southern Balkan Peninsula, occurs on a serpentine formation, it is not known whether it is restricted to serpentine. Another Old World endemic reported to occur on serpentine is *C. gymnopus* of Hokkaido Island in the Japanese Archipelago. In North America the oldest species in their respective groups, *C. monticola* and *C. pleurocarpa*, have their "diploid" (22-chromosome) forms confined to the Mesozoic and Paleozoic rocks of the Klamath Mountains in northern California; and diploid *C. pleurocarpa* has been found only on serpentine and similar formations. Here is at least an indication that the restricted distribution of some of the primitive endemic species of *Crepis* is due, in part at least, to their peculiar edaphic requirements.

A similar relation between edaphic restriction and distributional restriction is found in such primitive endemics as *C. terglouensis*, *C. albiflora*, and *C. dioritica*. These species, like several other alpine relics, which occur locally but have somewhat wider distributions (*C. pygmaea*, *C. rhaetica*, *C. Jaquini*, *C. pontana*, *C. blattarioides*), are restricted to calcareous formations; whereas some of the most widely distributed primitive species (*C. paludosa*, *C. conzaefolia*) have been reported as occurring on both calcareous soils and soils deficient in lime.

THE BEARING OF ENDEMISM IN CREPIS ON PLANT DISTRIBUTION AND ON THE NATURE OF SPECIES

In addition to the support found in this study of endemism in *Crepis* for the phyletic history of the genus as a whole, it appears that some of the evidence on *Crepis* endemics has a significant bearing on certain problems of plant distribution and the nature of species.

Crepis and the age-and-area concept.—One distributional problem concerns the well-known age-and-area hypothesis (Willis, 1940) which assumes that the age of a species or group is proportional to the area it occupies (under certain specified conditions; cf. Gleason, 1924). From the foregoing review it is clear that among the endemic species of *Crepis* there are two extremely diverse groups: (1) the primitive, perennial alpine endemics, which are relatively old, monomorphic, and adapted to mesophytic conditions; and (2) the advanced, annual, lowland endemics, which are relatively young, more highly variable, and adapted to xerophytic conditions.

The present distribution of these two groups does not conform to the age-and-area hypothesis. The old, alpine endemics, however, are believed by most students of floristics to have been more widespread before the Pleistocene epoch and to have moved, from glacial refugia, into the narrow niches that they now occupy (Braun-Blanquet, 1923, pp. 260-261). The fact that many of them are of relatively wide distribution, although they exist only in a special type of environment, supports this idea. On the other hand, the young, lowland, annual endemics are just as widely distributed as the alpine species are at present; and there are a number of lowland, annual species, not endemics, *C. foetida* and *C. pulchra*, for example, which are about as widely distributed as the forerunners of the alpine endemics ever could have been. Hence, the age-and-area concept breaks down completely with respect to these two groups of endemic species. As has been pointed out by Stebbins (1942a), the concepts of "senescence" and "competition" are no more satisfactory than age-and-area in attempting to account for such diverse groups of species. But the concept that the monomorphic, alpine species are genetically homogeneous and that the variable, lowland species are genetically heterogeneous, i.e., composed of several or many biotypes, provides an acceptable explanation of their differences in variability and distribution.

*The nature of the "narrow" *Crepis* endemics.*—This genetic approach to the problem of the differences between the widely distributed alpine and the lowland endemics also provides a satisfactory explanation of the nature of the "narrow" *Crepis* endemics. Of the forty-eight Old World species which were classified as "narrow," many are known only from their type locality or from vague information about their distribution. But there are several concerning which it is possible to make fairly definite statements. In their phylogenetic groups, these species, together with pertinent data, are as follows.

NARROW ENDEMICS—ALL PRESUMABLY MONOMORPHIC

Primitive

1) *C. kilimandscharica*. Section 8. Known only from Mt. Kilimanjaro at four stations, 2,700–3,500 meters, in forest.

2) *C. cameroonica*. Section 8. Known with certainty only from Mt. Cameroon at three stations, 2,000–4,000 meters, in meadows.

Intermediate

3) *C. taygetica*. Section 10. Known from five collections, all made at a place called "Porta," at about 2,300 meters altitude on Mt. St. Elias in the Taygetos Mts. of southern Greece. Exposed rocks.

4) *C. crocifolia*. Section 10. Known from three or four collections made at a place called Megala Zonaria, at about 2,400 meters altitude on the same mountain as the preceding. Exposed rocks.

5) *C. athoa*. Section 10. Seven collections, all on Mt. Athos, Hagion Oros Peninsula, northern Greece. Exposed rocks.

Advanced

6) *C. eritreensis*. Section 20. Three or four collections at localities in southern Eritrea from 800 to 1,400 meters elevation. One collection was from "a comparatively moist, rocky formation."

7) *C. tybakiensis*. Section 20. Known from one specimen collected in southern Crete. Since Crete has been botanized by numerous collectors, it is very probable that this species would be represented by more collections if it were widely distributed on the island. Certainly insular.

8) *C. divaricata*. Section 25. The population on Madeira Island is restricted to the isolated eastern promontory, where it has been nearly exterminated by grazing. (This species, considered as a whole, is classified as polymorphic in table 1 because of the variant specimens collected in 1837–1850 from the tiny Desertas Islands near Madeira.) Certainly insular.

9) *C. Noronhaea*. Section 25. Six collections, all from Porto Santo, a small island in the Madeira Archipelago. Certainly insular.

10) *C. Forskalii*. Section 27. Two localities in Yemen province, southwestern Arabia, between 1,300 and 2,500 meters elevation, in the coffee belt.

It is noteworthy that three of these species, *C. divaricata*, *C. Noronhaea*, and *C. tybakiensis*, are insular and of very restricted distribution. They are, however, relatively advanced species. Therefore, their morphological homogeneity (assuming that *C. tybakiensis* is actually monomorphic) must be due to genetic homogeneity rather than to senescence. Five others in the above list, *C. kilimandscharica*, *C. cameroonica*, *C. taygetica*, *C. crocifolia*, and *C. athoa*, are each found on only a single mountain. They are almost certainly "depleted" species (Stebbins, 1942a), and they probably became isolated through widespread changes in topography and climate during late Tertiary and Pleistocene times. In these, also, the population must be relatively small and homogeneous. The other two species, *C. eritreensis* and *C. Forskalii*, may also be "depleted" species, although it must be admitted that the available information on their distribution and variability is scanty. It is probable that all of these narrow endemics had their origin in Tertiary times or not later than Pleistocene (see p. 109). Therefore, since they are not of relatively recent origin, the genetic view that they are descendants of populations which were formerly more widespread, and that restriction of area has been accompanied by depletion of biotypes and genes, seems the most reasonable concept of their nature. It has been pointed out to me by M. K. Elias (*in litt.*) that the concept of "senescence" is hardly a realistic concept, since it is based on analogy, not on homology, with the life cycle of an individual. He also suggests that *Crepis* may be in a stage of "contraction" in the sense of Simpson (1940). Although this idea is hardly applicable to the genus as a whole, it may apply to certain sections or to certain types of species, such as the narrow endemics. Because the narrow *Crepis* endemics, both the insular and the continental species, are not "young" species in the sense of Willis, they do not conform to the age-and-area hypothesis any better than the two groups of widespread endemics discussed above.

SUMMARY

- 1) The twelve endemic regions for *Crepis*, comprising twenty-five areas, define the east-west distribution of the genus in the Old World almost completely.
- 2) Seventy-two per cent of the Old World *Crepis* species are endemic in the sense that they are restricted to a single subcontinental geographic area. Among these endemic species are two very diverse groups, namely, the most primitive, perennial species, half of which are alpine relics, and the advanced, annual species, most of which occur at low altitudes under arid conditions. The remaining endemics comprise an intermediate series connecting these two extremes. Only a comparatively few of the alpine perennials and the lowland annuals have narrow distributions, i.e., their distributional areas, as at present known, are mostly more than 150 kilometers in extent. From this evidence it is inferred that the alpine relics were formerly of wider distribution and that they moved into their present niches from glacial refugia; whereas the lowland, annual endemics have become adapted to a more arid climate, under conditions, however, favoring genetic heterogeneity. From the evidence on morphology and distribution, as well as on chromosome numbers, it is inferred that the process of adaptation from mesophytic to xerophytic conditions went on in the genus as a whole over a long period of time.
- 3) The distribution of the most primitive and the most advanced endemic species of *Crepis* supports the conclusion, derived from the evidence on phylogeny and distribution of the genus as a whole, that the center of origin was in Central Asia.
- 4) The age-and-area concept of Willis is completely at variance with the evidence on the two diverse groups of widespread endemic species mentioned above.
- 5) The concept of "senescence" fails to explain the existence of narrow endemics in *Crepis*, since this group includes some of the most primitive and most advanced species in the genus. Since they are either insular or "depleted" continental species, the population is more or less restricted in size and is relatively homogeneous. They also fail to conform to the age-and-area hypothesis.

CHAPTER 8

THE ORIGIN, MIGRATIONS, AND EVOLUTION OF CREPIS

THE PRESENT distribution of *Crepis* is of general interest in connection with the floristic history of the world, since it involves not only the Northern Hemisphere and the eastern continent (Eurasia), but also Africa and North America. Hitherto, the relation of this genus to vegetational history has not been recognized because (1) the genus has not been studied previously as a whole, and (2) the significance of the few fossil specimens of *Crepis* at present available (see pp. 132-134) has not been recognized. The dangers of basing phylogenetic assumptions only on the morphological relations and geographic distribution of existing species are well known. But when the systematic treatment of a unit-group rests on the synthesis of evidence from several different disciplines, and these various lines of evidence are all consistent with one another in their phylogenetic implications, as well as with the fossil evidence, which is true in *Crepis*, then surely one is warranted in erecting a hypothesis concerning the most probable region of origin of the group, its approximate age, and the probable migration routes over which it was distributed in order to explain its present distribution. All this, provided, of course, that the hypothesis can be shown to be consistent with the general principles of earth history and plant development as established by the known facts of geology and paleontology, especially paleobotany.

The earlier concept of the present author (Babcock, 1936), that the center of origin of *Crepis* and its closest allies was probably situated in southwestern Asia, was based on less complete evidence than is now available and without attempting to correlate the evidence on *Crepis* with the known aspects of vegetational history in the Northern Hemisphere, particularly in Eurasia. This correlation has now been established, with the result that the center of origin of *Crepis*, and of many closely related genera, appears to have been situated in the northern part of Central Asia, more specifically in the Altai-Tien Shan Mountains and adjacent steppes and plains. Having already reviewed the chief lines of evidence on which this conclusion is based, the present chapter will present an outline of the probable course of development of the genus. But first it is necessary to consider two pertinent questions: (1) Is *Crepis* really an ancient genus? (2) How well adapted is *Crepis* to plant migration?

THE ANTIQUITY OF CREPIS

From the preceding review of the geographic distribution of the Crepidinae, it is obvious that this subtribe must have originated before the Pleistocene age. The world-wide distribution of *Hieracium* is enough in itself to establish this fact. During Pleistocene, especially in the time of maximum glaciation, the holarctic spread of many species and the extension of the subgenus *Stenotheaca* into North and South America could not have occurred. It is probable, as shown by Engler (1879), that the holarctic distribution of *Hieracium* occurred in post-Pleistocene times. But that the spread of the subgenus *Stenotheaca* from Asia via North America to the southern tip of South America and the development of the derived subgenus *Mandonia* in the Andes could have been accomplished in such a relatively short time is unthinkable, even in plants with wind-borne seeds. Hence, in formulating a hypothesis, we are forced to go back at least to the Tertiary period. The present distribution of several other large genera of the Crepidinae, such as *Prenanthes* and *Lactuca*, indicate a corresponding antiquity.

In *Crepis* the distributional evidence agrees completely with the foregoing. Sharsmith (1940) concluded that *C. nana typica* reached the Sierra Nevada of California between the Pliocene and the Wisconsin stage of the Pleistocene (see p. 140). On this basis it is safe to assume that its origin in Asia occurred as early as the Pliocene or earlier. It was shown by Babcock and Stebbins (1938, pp. 34-36) that the period during which the eight diploid, 11-paired North American species could have originated and migrated into the region they now occupy is limited to Miocene, Pliocene, and early Pleistocene; also, that the four older species probably originated about the middle of this period, i.e., in late Miocene, whereas the four younger species were most probably formed during the latter part of the period, i.e., in mid-Pliocene or early Pleistocene time. Since it is practically certain that all these species originated through hybridization between diploid Asiatic species with lower chromosome numbers, it is fairly certain that the most primitive species of *Crepis* had their origin at least as early as Middle Miocene. But the gap which exists between these most primitive *Crepis* species and their putative ancestors in *Dubyaea*, both in their morphology and in their chromosome numbers and karyotypes, must indicate a developmental period of considerable length. Hence, the period during which *Dubyaea* flourished and during which the main phylogenetic lines of the Crepidinae had their origin and early development, may safely be considered to be as early as the beginning of the Miocene epoch. They may have existed even in Oligocene or late Cretaceous. The possible correlation of the history of the Crepidinae with that of the Artiodactyls (see p. 133) suggests such an early origin for the ancestors of *Crepis*. Since, however, the Miocene epoch has been estimated by various authors to have lasted from twenty to thirty million years, it would seem hardly necessary to go further back than late Oligocene for the origin of *Crepis*.

Fortunately, there is some fossil evidence which establishes beyond much doubt the existence of *Crepis* in the Tertiary period. Reid and Reid (1908, 1916) reported seeds of three species of *Crepis* from the Middle Pliocene Reuverian beds at Swalmen and Reuver in southeastern Holland, near the border of Germany; also, of one species from the Upper Pliocene Cromerian beds at Pakefield, Suffolk, England. Three of these four fossil species have been definitely identified. These are illustrated in plate 1, along with present-day achenes of the same species. (The fourth species was identified by Reid and Reid [1916] as *Crepis fuscipappa* [now *Youngia fuscipappa*] and, along with the one fossil seed [in their pl. 17, nos. 28, 29], was shown, as supposedly corroborative evidence, a present-day achene of *Youngia cineripappa* Babc. et Stebbins from China. But *Youngia fuscipappa* occurs only in Ceylon. This fossil seed is very probably not a species of *Youngia*, since that genus is restricted to eastern Asia. Judging only from the lithograph, this fossil is not well enough preserved to make identification possible, although it may be a species of *Crepis*.)

In plate 1, *a* and *a'* show one fossil and two present-day achenes of *Crepis terglouensis*. This fossil was originally reported as *Crepis* sp. by Reid and Reid (1916, pl. 17, no. 30), who must have had no present-day achenes of this species with which to compare the fossil, because the resemblance is perfect in every observable detail. Even the cracked and flattened base of the fossil achene, which at first glance appears broad and notched, would correspond with the rather narrow base in the perfect achenes, if it could be restored. In plate 1, *b* and *b'* show two fossils and two present-day achenes of *Crepis conyzaeifolia*. The two fossils were identified as *C. blattarioides* (Reid and Reid, 1916, pl. 17, nos. 26, 27). Although they fall within the size range of that species, the ribs are too few and much too wide for *C. blattarioides*, whereas they very closely resemble those of *C. conyzaeifolia*; also, the over-all size is within the range of this species.

These fossils of *C. terglouensis* and *C. conyzaefolia* were found in the Reuverian beds in southeastern Holland, which formation was identified by Reid and Reid (*op. cit.*) as most probably Middle Pliocene. That district, according to the authors, was included in the extensive delta of the Rhine and Maas rivers during certain parts of the Pliocene epoch. These great rivers evidently brought down from the northern slopes of the Alps vast quantities of plant material which were deposited in the estuary. Along with seeds and fruits of hundreds of other species, these *Crepis* fruits were recovered from the clay pits of Limburg and near-by Germany.

The third *Crepis* species which is represented by a reported fossil is *C. mollis* (*C. succisaefolia* of Reid and Reid [1908, p. 217, pl. 13, no. 96]). Fossil seeds of this species were reported as not uncommon at Pakefield, where they were found in clay deposits determined to be Upper Pliocene. *C. mollis* is a widespread species of central and northern Europe and occurs at the present time in England. The fossil achene is reproduced in plate 36, *c*, and, with it, *c'*, are two present-day achenes. The resemblance is very close. The fossil specimen falls within the known range of length, but it is a little broader than the broadest achene of this species available to me, and the ribs, though the same in number, are somewhat wider. It might well be assumed that the differences mentioned are due to the reduction in width of fruits and ribs which has accumulated in this species during the Quaternary period.

It should be mentioned that fossil achenes of *Crepis capillaris* have also been reported (as *C. virens*) by Reid (1898, 1899) as occurring in late Glacial and Neolithic deposits in Scotland.

The fossil fruits of *C. terglouensis*, one of the most primitive 6-paired species, and of *C. conyzaefolia*, the most primitive 4-paired species, are especially significant in establishing the age of *Crepis*. The fact that these species existed on the northern slopes of the Alps in pre-Pleistocene times, and probably as early as Middle Pliocene, calls for a considerable interval of time during which they could have migrated from Central Asia, a straight line distance of more than 6,000 kilometers. In view of this evidence it is necessary to assume that *Crepis* originated at least as early as the Miocene epoch.

This assumption is in good agreement with the general scheme of phylesis in the Compositae by Small (1919, p. 297), in which he shows the Lactucinae (=Crepidinae) as differentiating into subtribes in Miocene. Furthermore, Small (*op. cit.*, pp. 321-326) emphasizes the importance of the Miocene epoch for the differentiation of the Compositae throughout the world, by stating that at or before Middle Pliocene most of the subtribes of the Compositae had been differentiated and that Upper Pliocene and later times were characterized by generic, specific, and varietal differentiation rather than by the origin of larger groups.

Significant, if true, is the paleogeographic evidence found in the Miocene continental outlines (cf. fig. 6, lower map). The broad peninsula extending from Central Asia westward into Tethys as far as the European Alps, and the continuous land across Arabia to Africa, provided land routes for the most primitive species of *Crepis* into southern Europe and tropical Africa during Miocene.

An established fact of possible significance for the antiquity of *Crepis* is the present occurrence of certain primitive, endemic species (*C. geracioides* of Albania, *C. gymnopus* of Japan, and the 22-chromosome form of *C. pleurocarpa* of northern California) on serpentine formations. Furthermore, those formations on which *C. pleurocarpa* is found are associated with other Mesozoic and Paleozoic rocks.

In this connection it may also be significant that in a recent and thorough evaluation of the evidence bearing on the origin and distribution of the Artiodactyl

ungulate mammals Pilgrim (1941, pp. 153-156; 161-162) concludes that the sub-order Pecora, which includes such ruminants as deer, antelopes, goats, sheep, oxen, and giraffes, had its origin in Central Asia, from whence it spread over the world. The pecoran families, according to Pilgrim, branched off from the more primitive Tragulina probably in the Oligocene epoch. If this is true, they must have been developing and migrating throughout the Miocene. Pilgrim (*op. cit.*, p. 155) refers to Miocene fossils from Europe, Mongolia, and North America which support this inference. Many species of *Crepis* are associated today with grasses and other herbs of importance as forage for ruminants; and some *Crepis* species are so acceptable to sheep and cattle that botanical specimens are sometimes extremely difficult to find on areas that have been grazed recently. It is not unlikely, therefore, that the development and migrations of the Crepidinae were contemporaneous with, or antedated, the development and migrations of the Pecora from Central Asia throughout the world.

In view of all the evidence, the conclusion is warranted that *Crepis* had its origin, early dispersal, and beginnings of differentiation about the middle of the Tertiary period, either in early Miocene or late Oligocene.

THE ADAPTABILITY OF CREPIS TO MIGRATION

As was pointed out by Engler (1916), plant migration is generally dependent on the germinability, viability, and transportability of the seeds, as well as the existence of favorable environmental conditions in the region invaded. Most *Crepis* species reproduce exclusively by seeds, and in those few which are mat-forming or which reproduce by stolons, viable seeds are also produced. Although some of the high montane, primitive species have proved rather difficult to propagate from seeds under artificial conditions, yet where it has been possible to imitate natural conditions rather closely the seeds have usually germinated satisfactorily. Only in *Crepis pygmaea* has it not yet been possible to obtain plants from seeds collected the previous year in the Alps, although several attempts were made; as a result, our cultivated specimens had to be grown from roots collected in the wild. It happened, however, in *C. pygmaea* that the best method of germinating the seeds of alpine species—subjecting the seeds to more nearly natural conditions by placing them outdoors in a flat at a montane elevation where they would be covered by snow in the winter, with consequent spring thawing and freezing—was not used. It is probable that seeds of *C. pygmaea* would have germinated under such conditions.

Great variation exists with respect to the length of viability of the seeds of *Crepis* species. It is safe to assume, however, that the seeds of all species remain viable for at least one year, since it has been possible to propagate many of the species from seeds more than one year old. In this connection the difference between *C. capillaris* and *C. tectorum* in seed viability is of considerable interest. Navashin, Gerassimova, and Belajeva (1940) reported a striking difference between the two species in the effect of storage on germinability of the seeds and viability of the seedlings. At the end of two and a half years all the seeds of *C. tectorum* had nearly lost the ability to germinate, and the viability of the few seedlings obtained was almost nil, whereas the seeds of *C. capillaris*, as had been observed in early experiments, showed much greater resistance. The distinction between the two species, it was pointed out, is an important adaptation. *C. capillaris* is a typical annual, and its achenes normally germinate in the spring after a period of eight or nine months of dormancy, whereas *C. tectorum* is a "winter plant," i.e., its seeds germinate soon after maturation, the vegetative rosettes live through the winter even in Russia, and the plants

flower the following spring or early summer. It will be noted, however, that even in *C. tectorum* the seeds retain their viability for two years in sufficient degree to maintain the species. Perhaps the most striking correlation between high specialization and length of seed viability is found in *C. seneciooides*, a precocious desert annual the tiny seeds of which remain viable for at least twelve years and possibly longer.

As for transportability, the seeds of most species of *Crepis*, with their abundant pappus, are especially adapted for transport by wind. In the most primitive species the seeds are light and the pappus is relatively large. Even in *C. kashmirica* the very coarse ribs of the achenes are merely folds enclosing white, spongy tissue; and a single dry seed, containing an embryo, weighs only about two milligrams. In a gentle breeze, such a seed, even with its pappus intact, tends to fall rapidly toward the earth; but in a strong wind it is possible for it to be carried great distances. Hegi (1929) reports the observation of an immigrant colony of *C. alpestris* in a newly excavated gravel pit to which the achenes must have been carried at least three kilometers distance from the nearest mother plants. *Crepis* is classified by Ridley (1930) as being dispersed by wind, by adhesion to animals, and by human agency. He also states that the seeds can be dispersed by water, since he observed seeds of *C. biennis* remaining afloat for one and a half days. In *C. patula*, which has extremely short pappus, the seeds remain enclosed in the strongly indurate involucre. This species often grows on stream banks, and it is probable that old, broken-off involucres full of seeds are sometimes transported by the streams. The same might be true of its close relative, *C. Zacintha*. Ridley reports no evidence on dispersal of *Crepis* by birds, but *Taraxacum* is mentioned in one such list. It is possible that some of the wider gaps in distribution among the primitive species found on the high mountains of tropical Africa would best be explained through dispersal by birds. But, in addition to all other natural methods of seed distribution in *Crepis*, dispersal by wind is undoubtedly efficient enough to account for very extensive migration and for wide gaps in distribution.

Concerning wind dispersal in the Compositae as a whole, Small (1919) concludes that the evidence from Krakatau is confirmed by the observations on Taal Island (in Bombon Lake, Luzon) and that there remains no doubt whatever about the usual dispersal by wind of a number of Compositae to distances of 4 to 20 miles and the occasional dispersal of pappose fruits to distances of more than 100 miles. Small (*op. cit.*, 169-177) conducted a critical experiment on the aerodynamics of fruit dispersal in *Taraxacum officinale* from which he concluded that the conditions necessary for long distance dispersal of seeds are: (1) low relative humidity of the atmosphere; (2) a wind constant in direction and always above a certain minimum velocity (for dandelion seeds, about 2 miles per hour). He concludes that, given these conditions, there is no limit to the dispersal of pappose fruits. He states further that such conditions occur occasionally in most of the regions in which long-distance dispersal has been observed. There would seem to be little if any doubt that such conditions must have existed occasionally during periods when *Crepis* fruits would have been ready for dispersal throughout southwestern Asia and northern Africa. It is possible, therefore, that *Crepis* species were distributed by wind from one mountain to another across tropical Africa, or from one range to another across northern Africa, and even from the African mainland to the Madeira and Canary Islands, distances of 100 and 700 kilometers, respectively (about 60 and 400 miles). The conclusion of Cockerell (1928) that seeds were carried from the mainland to the Madeira Islands by birds appears to be warranted, since the distance from the mainland is small and no less than seventy species of birds have

been reported as visitors or stragglers to Madeira. But the evidence of Danish investigators (cf. Warming, 1903, p. 676) is definitely against such a conclusion being applied to the Canary Islands.

The relative importance of the wind and all other possible agencies in establishing the present flora of the Faeröes, the group of small islands lying 400 kilometers (nearly 250 miles) north of Scotland, received careful consideration by Warming (*op. cit.*), whose studies on the floras of isolated north Atlantic islands are outstanding. He reaches the general conclusion that the whole of the flora—at least all the more highly organized land plants—have migrated to the Faeröes since the glacial period, across the sea, and from the nearest countries, especially Great Britain. Man, he points out, has undoubtedly been responsible for the introduction of the weeds and some of the other lowland species. But at least 60 per cent of the vascular species must have depended upon other agencies for transportation. Although a few species may have been brought by ocean currents, and some others, especially those with heavier seeds, possibly by birds, yet it seems probable that the wind was the most important agency in transporting the seeds of most of these plants. Regarding the general importance of winds as an agency in plant distribution, Warming (*op. cit.*, p. 679) reaches the conclusion that "On the whole I am unable to find an explanation for the different phenomena respecting the distribution of plants, unless I adopt the theory that germs of all kinds are being sown constantly and in every direction, and that it is chiefly by the agency of the wind that the sowing and colonization of the earth is effected across longer distances."

ECOLOGICAL RELATIONS OF CREPIS

The ecological relations of *Crepis* are extremely varied. But, for purposes of the present discussion, the species can be roughly classified by sections according to temperature and moisture relations as follows :

- A. Temperate, mesophytic—sections 1, 5, 7, 8.
- B. Temperate-alpine, mesophytic—sections 3, 6.
- C. Alpine or arctic-alpine, mesophytic—sections 2, 4, 12.
- D. Temperate, mesoxerophytic—sections 9–11, 13–21, 23–25.
- E. Temperate, xerophytic—sections 22, 26, 27.

Almost all of the species are adapted to a temperate climate, and the most primitive ones (secs. 1–8) are definitely mesophytic. Among these primitive species there are several, most notably those of sections 3 and 6, with wide altitudinal ranges, i.e., they occur in locations ranging all the way from temperate (or even warm-temperate) up to alpine climates. The same is true to a more limited extent for *C. sibirica* and *C. paludosa* of section 1. These wide altitudinal ranges certainly indicate a marked adaptability in these species which is directly correlated with such wide geographic distributions as those of *C. sibirica*, *C. paludosa*, and *C. conyzæfolia*. When these species are found in subalpine or alpine locations, it may be assumed (cf. p. 103) that in some earlier epoch climatic conditions favored their migration upward, from a more extensive distribution at lower altitudes, and that subsequent environmental changes resulted in the establishment of local alpine populations (cf. *C. pygmaea*, Part II, p. 242). In such a species as *C. rhaetica* and the strictly alpine species of sections 2 and 4, the same sort of earlier history can be assumed, except that subsequent climatic changes completely exterminated the forms of these species which existed earlier at lower levels. This Englerian hypothesis, which has been accepted by Braun-Blanquet (cf. p. 104) and many others, is accepted here as the best explanation of the present distribution of the alpine endemics in *Crepis*. In the more advanced sections there is an increasing number

of xerophytic species which is directly correlated with the fact that these species were differentiated in south Central and southwestern Asia and the Mediterranean region during Pliocene-Pleistocene at times when these regions became extremely arid. This sweeping statement applies only in a general sense. In all of the more advanced groups (secs. 9-27) we find more or less variation between the species of a section with respect to water relations, indicating that they evolved under various local conditions.

ORIGIN, MIGRATIONS, AND DEVELOPMENT OF CREPIS

Origin.—Like the other primitive generic types in the Cichorieae, the earliest *Crepis* species probably developed from *Dubyaea*-like species which had already evolved from less specialized ancestors living in northeastern Asia (Angara). That the progenitors of *Dubyaea* could have originated somewhere east of Lake Baikal and moved westward into the Altai region is not an unreasonable hypothesis. Although there is available to me no present-day or fossil evidence to support the idea, yet it is in line with the observation of Kryshtofovich (1933, p. 121) that in the Ussuri region, north of Vladivostok, there is clear evidence that in Lower Cretaceous time there began a new development of plant life. He suggests that this came about through the immigration of new elements which had developed in or near the glaciated region (to the north, see p. 93) and which united with the Paleozoic flora of Angara to give a new start to the plant world.

The closest living relatives of these assumed ancestors of *Crepis* are the most primitive species of *Dubyaea* (cf. Stebbins, 1940, p. 52), namely, *D. oligocephala*, *D. hispida*, *D. atropurpurea*, and *D. chilensis*, the first two of which are known to have 8 pairs of chromosomes (Babcock, Stebbins, and Jenkins, 1937). It is assumed that in the *Dubyaea*-like ancestors of *Crepis* the chromosome number had already been reduced from 8 to 7, since the most primitive *Crepis* species have 6 and 5 pairs of chromosomes.

It is probable that these earliest *Crepis* species developed in the Altai-Tien Shan region of Central Asia. This hypothesis is based on the present geographic distribution of *Crepis* and related genera. This American-Asiatic-European-African distribution resembles that of many other genera, some of which, like *Cedrus* and *Datisca* (pp. 98-100), appear from the fossil evidence probably to have originated in Asia. Strong precedents are found for accepting this hypothesis in the conclusions reached by Engler (p. 102) regarding *Aconitum*, *Pedicularis*, *Saussurea*, and many other genera; by Schwarz (p. 106) for *Laurentia tenuella*, *Pinus Peuce*, and other species; by Czeczkott (1937) for *Datisca cannabina* and other Colchic-south Euxine plants; and by Hagen (p. 107) for a great many xerophytic species that migrated from Asia into north Africa. For reasons already stated (pp. 131-134) it is probable that these earliest *Crepis* species appeared about the middle of the Tertiary period.

Early development.—1) The rhizomatous species.—The most primitive species, *Crepis sibirica*, *C. geracioides*, *C. viscidula*, and *C. paludosa* (sec. 1), have a rhizome instead of a true root; and since they now occur in a temperate climate and in moist locations, it is assumed that their *Dubyaea*-like ancestors inhabited moist places in the lower montane regions. The other primitive rhizomatous species (sections 2, 3, 4, and 5) probably had a relatively early origin, since, even though their development occurred under a variety of conditions, they all contain 6-paired species. The species of sections 2, 3, and 4 became adapted to much higher elevations in the mountains and to various types of soils; whereas the more primitive species of section 5, *C. lapsanoides*, *C. lyrata*, and *C. mollis*, occupied habitats more like

those of section 1. Similarly with section 13, *C. gymnopus* became differentiated in connection with adaptation to alpine conditions, whereas *C. praemorsa* is a low-land species. Three of the species in section 21 are alpine or high montane and the other one, *C. Gmelini*, occurs in eastern Siberia at about the 60th meridian. All four of these species have become adapted to much colder climates than those suitable for sections 1 and 5.

2) The primitive taprooted species.—The taprooted species probably developed from rhizomatous ancestors. Evidence for this has been presented (pp. 43, 70) in connection with *C. rhaetica*, *C. Reuteriana*, and *C. Bungei*. Furthermore, a marked resemblance was noted between *C. pontana*, the most primitive taprooted species, and the species of sections 1 and 2. It seems very probable that the early types with a deeply penetrating taproot became established in connection with adaptation to drier situations. At any rate, the other species of section 6, like *C. pontana*, came to occupy high montane habitats. Furthermore, the section 2—section 6 line seems to have developed in the southern part of the region of origin, whereas the foundation stock of section 4 began rather early to spread both to the northeast and southwest. In the more southern part of the general region of origin, also, the progenitors of sections 7, 8, 9, 10, and 11 must have begun their development during this earlier period in the history of the genus.

3) The probable status of the genus in early Miocene.—From the foregoing considerations (chaps. 4–7) and evidence given under individual species (Part II), it may be assumed that in the early part of the Miocene epoch the more primitive rhizomatous species were already differentiated into geographical and ecological groups. *C. sibirica*, *C. paludosa*, and *C. mollis* were probably abundant at lower elevations between the Altai and the Ural Mountains; whereas *C. geracioides*, *C. viscidula*, *C. pygmaea*, *C. lapsanoides*, and some other members of section 6 were probably distributed in the southwestern part of north Central Asia at various elevations. *C. hokkaidoensis*, *C. chrysantha*, and *C. gymnopus* were already distributed at high elevations toward the northwest. Certain species, *C. terglouensis*, *C. Jacquinii*, and *C. rhaetica*, which are now relies in the European Alps, were probably distributed at high elevations in the southwestern part of the region of origin; whereas *C. pontana*, *C. conyzaeifolia*, *C. blattarioides*, *C. aurea*, *C. albida*, and *C. tingitana*, as well as *C. kilimandscharica*, *C. alpestris*, and their closest relatives in section 8, occurred at somewhat lower elevations in the same region.

By late Miocene the more primitive species of several other sections were probably established mostly in the Tien Shan–Betpak-dala uplands, such as *C. Strausii*, *C. darvasica*, *C. songorica*, *C. sonchifolia*, *C. auriculaefolia*, and *C. Raulini* of section 10; *C. Schachtii*, *C. Hookeriana*, *C. bithynica*, *C. armena*, and *C. tenerrima* of section 11; *C. connexa* of section 16; *C. Reuteriana* of section 19; *C. alpina* of section 20 or a less-specialized form of it; and *C. patula* of section 23. But *C. oreades* of section 11 and *C. Bungei* of section 14 were distributed more to the east.

Sections 12, *Ixeridopsis*; 15, *Psilocheenia*; and 18, *Pyrimachos*, require separate treatment. The *Ixeridopsis* group, one member of which, *C. nana*, is now distributed from south Central Asia to northeastern North America, probably originated in the Tien Shan region as early as the most primitive species of *Crepis*. It seems probable that the whole group originated through hybridization between one or more *Crepis*-like *Dubyaea* species and one or more *Ixeris*-like *Dubyaea* species, all of which had 7 pairs of chromosomes. The indigenous North American species, section *Psilocheenia*, are believed to have originated through several different hybridizations involving species in sections 2, 4, 11, 12, 13, and 14, or similar now-extinct species. It is probable that all of these putative ancestors of the American

group were distributed in the eastern part of the region of origin or had already migrated farther to the northeast before hybridization occurred. Pyrimachos, section 18, may have arisen independently from the ancestral stock from which *Ixeris*, *Youngia*, and *Crepis* arose, or from hybrids between these lines before they were sharply differentiated. In either event, their origin probably occurred in the southern part of the region of origin of *Crepis*. The probability that this is true is considerably increased by the fact that both *Ixeris* and *Youngia* have their present distribution for the most part in E. and S.E. Asia.

Migration and later development.—1) East-west migration from north Central Asia.—After the region southeast of the Ural Mountains had emerged from beneath the Obic Sea and the higher Kirghiz steppes were thus extended westward into "Russia," *C. sibirica*, *C. paludosa*, and *C. mollis* could spread over northern Europe. The last two species were much more aggressive than *C. sibirica*, which may never have reached the Atlantic coast. With increasing cold during Pliocene, these species all moved southward, *C. paludosa* and *C. mollis* eventually finding Pleistocene refugia in southern Scandinavia, the British Isles, and the southern mainland; whereas *C. sibirica* was limited to a few localities in the Sudeten-Carpathian region. It was probably during the cooler Pliocene epoch that the alpine *C. multicaulis* migrated across the Urals and arctic Russia to northern Scandinavia where it persisted as a nunatak species during Pleistocene. About the same time, *C. praemorsa* moved both eastward across Siberia and westward into Russia, across the Ural-Caspian land area, and gradually extended its area to the west until it reached the southeastern Alps, where *C. incarnata* originated. Meanwhile, *C. pannonica* had originated, presumably in Betpak-dala, and followed a migrational course similar to the western trend of *C. praemorsa*, but somewhat more southerly. When it reached the northwestern Balkan Peninsula and Italy, probably in Pleistocene, it gave rise to *C. latialis*, *C. chondrilloides*, and possibly *C. bertiscea*. It may be that the progenitors of the two octoploid species, *C. ciliata* and *C. biennis*, also reached the Caucasus over a route north of the Caspian Sea. At any rate, the origin of these two polyploids probably occurred in the Caucasus Mountains during Pleistocene. Their ancestors are believed to have been related rather closely to the ancestor of *C. nicaeensis* (Part II, pp. 439, 769), and they may have been related to the ancestor of *C. oporinoides* of S. Spain (Part II, p. 474).

2) Northeasterly migration from Central Asia.—*Crepis sibirica*, in addition to its migration into Europe, also extended its range to the northeast and east of the Altai region. Also, *C. hokkaidensis*, *C. gymnopus*, and *C. chrysanthia* continued their northeasterly movement, the first two probably reaching their present localities during Pliocene or Pleistocene when what is now the Japanese Archipelago was still a peninsula extending south from Amur. These species, of course, found plenty of refugia along their route during maximum glaciation. The spread of *C. chrysanthia* over the arctic tundra into the Urals and northeastern Europe undoubtedly took place in post-Pleistocene time. Probably it was during this later epoch also that the tetraploid *C. polytricha* arose; also, that *C. Bungei* and *C. tectorum* of section 14 had their origin in Siberia from *C. irtutensis* or similar ancestors. The distribution of *C. oreades* of section 11 in its eastern extension probably overlapped that of *C. Bungei*; but *C. oreades*, being distributed much farther to the southwest than *C. Bungei*, eventually reached the Pamirs. In this respect *C. oreades* shows a tendency to follow the general migration trend of all the species in its section except *C. crocea*. The former is probably an amphidiploid derived from a hybrid between *C. crocea* and *C. Bungei*, and, like other aggressive polyploids, it was able to extend its range far beyond those of the parents, reaching Manchuria to the

northeast and Tibet to the south. The species which migrated into North America, *C. nana* of section 12 and the amphidiploid progenitors of section 15, undoubtedly moved across the Beringian land bridge at several different times. *C. nana*, because of its present stations in northeastern North America, was probably the first to cross from Siberia to Alaska and beyond. If the section *Ixeridopsis* did arise from hybrids between partly differentiated *Dubyaea* lines, their origin occurred earlier than mid-Miocene. The probable sequence of migrations of the older and younger foundation species of section *Psilochaenia* is reviewed by Babcock and Stebbins (1938, pp. 30-38).

3) The southeasterly migrations from Central Asia.—Of the *Crepis* species thus far discovered, only nine migrated in a southeasterly direction from Central Asia. These are *C. subscaposa* of section 8, the monotypic section, *C. napifera*, five species of *Pyrimachos* (sec. 18), and two species of section 21. Reasons have been given (p. 71) for assuming that *Pyrimachos* had a hybrid origin somewhat similar to that of section *Ixeridopsis*. It is therefore reasonable to assume that this group also originated rather early in the history of the Cichorieae, when *Crepis*, *Ixeris*, and *Youngia* were not sharply differentiated. And the region of origin of this section was probably in Central Asia, like that of *Youngia*. Being adapted to a warmer climate than most *Crepis* species, these species migrated to the southeast during Pliocene and found their way still farther southward during Pleistocene. The origin and migration of *C. napifera*, which now occurs in southwestern China and southeastern Tibet, is in general similar to that of *Pyrimachos*. It appears to have been an offshoot from a primitive *Dubyaea* line that resembled both *Crepis* and *Youngia*. In *C. subscaposa* a somewhat different situation holds. Although it has none of the distinguishing features of section *Pyrimachos*, it now occurs in the same general region as that group. Moreover, it belongs morphologically in section 8, which section, except for one species, *C. alpestris* of Asia Minor and southern Europe, is found entirely in Africa. It is necessary to assume, therefore, that *C. subscaposa* originated from the same ancestral stock that produced *C. kilimandscharica* and *C. urundica*, but that for some reason *C. subscaposa* migrated from southern Central Asia in a southeasterly direction instead of a southwesterly direction. Perhaps the parting of the ways took place in early Pliocene northeast of the Pamirs, and *C. subscaposa* found its way across Chinese Turkestan and Tibet during Pluvial times, whereas *C. alpestris* and the other primitive species of section 8 moved southwest across Russian Turkestan and Iran. It is not impossible that other species resembling those of section 8 may yet be discovered in southeastern Asia. That section 21 (*Microcephalum*) had its origin in Central Asia is practically certain, since *C. tibetica* and *C. elongata* occur in southeastern Asia, *C. Gmelini* in northeastern Asia, and *C. multicaulis* is distributed from the Himalaya to the Altai and in northern Norway.

4) The southwesterly migrations from Central Asia.—These migrations were by far the most important movements of *Crepis* species away from the region of origin, since they had the most profound effect on the present distribution of the genus. The general aspects of these migration trends, and their consequences for many groups of flowering plants, may be summarized as follows: (1) They continued over a very long time, including probably both the Mesozoic and Cenozoic eras. (2) Throughout this period migrations went on in two directions, i.e., from Asia westward and vice versa. (3) From mid-Tertiary onward the trend from Central Asia southwestward into the Mediterranean region and Africa became more and more pronounced. (4) During Pliocene and Pleistocene times the many topographic and climatic changes in southern Central Asia and the Mediterranean region re-

sulted in (a) the extinction in the eastern Mediterranean region of many of the more primitive types which had already become established in the Alps, the Iberian Peninsula, and the Atlas Mountains; (b) greatly increased speciation in those groups which still had representatives in the Turano-Iranian and eastern Mediterranean regions.

This increase in the number of species can be explained in terms of modern genetic theory. It is reasonable to assume, especially in plants well adapted for seed dispersal, that small subspecific populations would frequently become isolated in space at a given time. Also, isolation in time at a given place may have occurred as a result of sudden environmental changes. It has been shown by Wright (1931) that the effect of gene mutation, natural selection, and random fixation in a small population is the rapid reduction of genetic variability. It is highly probable that the genotypes fixed in different small populations of the same species would differ as a result of differences in mutations and environment. If the isolation of small subspecific populations were followed by the reestablishment of contacts between them through gradual expansion and overlapping of their continuous areas or through wind dispersal over intervening spaces, this would be followed by hybridization and the further operation of natural selection. Furthermore, the whole process might be repeated at a later period. Apparently the great increase in the number of species of *Crepis* in sections 8, 10, and 24–27 resulted from some such processes as the foregoing. The statement of Schwarz (1938), that the Armenian mountains served as a "gene filter" to reduce the number of biotypes in certain species, indicates his appreciation of the important role played by secular changes in the eastern Mediterranean region during Pliocene-Pleistocene in the evolution of the more advanced and specialized species of many plants, including *Crepis*.

The species of *Crepis* which migrated in a southwesterly direction from Central Asia may be divided into three groups. The first group consists of the more primitive species or more "aggressive" less primitive species that probably migrated during late Miocene or early Pliocene, reaching southern Europe and northeastern tropical Africa before the disruptive topographic and climatic changes in the eastern Mediterranean region could annihilate them. These species are listed below, each being preceded by its section number. The geographic distribution of each species is roughly indicated by the countries or regions in which it occurs. Names capitalized are the most primitive species in this group; names in lower case type are somewhat less primitive species.

GROUP 1

1. GERACIOIDES—N. Greece, Albania, Macedonia.
1. VISCIDULA—Albania, Serbia, Bulgaria, Rumania.
3. PYGMAEA—Tirol, Italy, Switzerland, France, Spain.
4. TERGLOUENSIS—Tirol, Austria, E. Switzerland.
4. RHAETICA—Switzerland, Tirol.
4. JACQUINI—Carpathians to Bavaria, Tirol, E. Switzerland.
4. aurea—N.W. Asia Minor, W. Balkan Peninsula to E. France.
5. LAPSANOIDES—Pyrenees, N. Spain, N. Portugal.
5. SMYRNAEA—N.W. Asia Minor, S. Greece.
5. montana—Greece.
5. Mungierii—Crete.
6. PONTANA—Bulgaria, W. Balkan Peninsula to Switzerland.
6. CONYZAEFOLIA—Altai, N. Iran, Asia Minor, Balkan Peninsula to Pyrenees.
6. BLATTARIOIDES—N.W. Balkan Peninsula, Tirol, Alps, Pyrenees.
7. ALBIDA—N.W. Italy, S. France, Spain, Balearics, N. Morocco.
7. achyrophoroides—N. Abyssinia.

8. KILIMANDSCHARICA—Mt. Kilimanjaro (Tanganyika).
8. KENIENSIS—Mt. Kenya (Tanganyika).
8. ALPESTRIS—N.W. Asia Minor, W. Carpathians, W. Balkan Peninsula, W. Austria, E. Switzerland.
8. SUFFRUTICOSA—Mt. Meru (Tanganyika).
8. IRINGENSIS—Mporotos Mts. (Tanganyika).
8. MERUENSIS—Mt. Meru, Mt. Kilimanjaro (Tanganyika).
8. CAMEROONICA—Mt. Cameroon (W. tropical Africa).
8. URUNDICA—Urundi (Belgian Congo).
9. TINGITANA—N.W. Morocco, S.W. Spain.
9. leontodontoides—N. Italy, S. France.
10. AURICULAEFOLIA—Crete.
10. BALDACCI—Balkan Peninsula.
10. RAULINI—Crete.
10. ALBANICA—Balkan Peninsula.
10. GUIOLIANA—Balkan Peninsula.
10. turcica—Balkan Peninsula.
10. Pantoesekii—Balkan Peninsula.
10. Triasii—Balearic Islands.
10. macropus—W. Asia Minor.
10. oporinoides—S. Spain.
10. Sibthorpiana—Crete.
10. incana—Greece.
10. taygetica—Greece.
10. crocifolia—Greece.
10. athoa—Greece.
11. SCHACHTII—S. Bulgaria.
11. BITHYNICA—Asia Minor, Bulgaria.
11. tenerrima—Abyssinia.
11. xylorrhiza—Abyssinia.
11. abyssinica—Abyssinia.
11. Hookeriana—Morocco.
11. Faureiana—S. Algeria.
11. Robertioides—Syria.
19. Reuteriana—S.W. Asia Minor, Cyprus, Syria, N. Palestine.
23. patula—N. Tunisia, E. Algeria.
24. nicaeensis—W. Balkan Peninsula, N. Italy, S.E. France, S. Pyrenees.
25. spathulata—Sicily.
25. Salzmannii—N. Algeria, N. Morocco.
25. Clausonis—N. Egypt, N. Tunisia, E. Algeria.
25. Fontiana—N.W. Morocco.
25. Bourgeaui—N. Morocco, S. Spain.
25. canariensis—Canary Islands.
25. divaricata—Madeira.
26. juvenalis—Tunisia.

The present distribution and probable origin of all these species are discussed under the respective sections in Part II of this monograph. Here, it is only necessary to point out that the first fourteen species in the above list (through sec. 6) apparently all followed the south-Euxine route, across northern Iran and northern Asia Minor into the Balkan Peninsula, where some remained, some moved northward, and some moved farther to the west. It is very probable that their arrivals in the west were spread over a long period. *C. albida* of section 7 also followed the south-Euxine route and finally reached northern Morocco via Spain, whereas *C. achyrophoroides* probably followed the route across southern Iran and Arabia to Abyssinia. With one exception, all the species of section 8 listed here probably also followed the southern Iran-Arabian route. The one exception is *C. alpestris*, which must have taken the more northern route across Asia Minor, as did also *C. tingitana* and

C. leontodontoides of section 9. In section 10, *C. auriculaefolia* and *C. Raulini* reached Crete, probably while it was still connected with the Balkan Peninsula; *C. Triasii* and *C. oporinoides* reached southern Spain, but none of the other species in this section got farther than the Balkan Peninsula. Of those in section 11, *C. Schachtii* and *C. bithynica* reached the Balkan Peninsula, *C. tenerrima*, *C. xylorrhiza*, and *C. abyssinica* reached Abyssinia, probably by way of the southern Iran-Arabian route, and *C. Hookeriana* and *C. Faureiana* reached the Great Atlas and Saharan Atlas Mountains, respectively, either by way of southern Europe or across north Africa from Abyssinia. The probable route of *C. Reuteriana* (sec. 19) is indicated by its present distribution. In section 23 *C. patula* probably came by the south-Euxine route, through Greece, and across the land bridge to Tunisia. *C. nicaeensis* (sec. 24) evidently came through northern Asia Minor to the Balkan Peninsula, but all the species listed from section 25, and *C. juvenalis* of section 26, probably took a more southerly route to maritime north Africa.

The second group consists of somewhat less primitive species which, because they failed for some reason to get through the Iran-Asia Minor region, remain as relict species in that general region.

GROUP 2

5. *willemetoides*—N. Iran.
7. *elymaitica*—W. Iran.
10. *Strausii*—W. Iran.
10. *darvasica*—Buchara (Turkestan).
10. *songorica*—Alatau Mts. (Turkestan).
10. *sonchifolia*—E. Caucasus.
10. *bupleurifolia*—E. Asia Minor.
10. *dens-leonis*—Caucasus.
10. *khorassanica*—N.E. Iran.
10. *turcomanica*—S.W. Turkestan.
11. *pinnatifida*—E. Asia Minor.
11. *heterotricha*—Iran.
11. *armena*—N.E. Asia Minor.
11. *demavandi*—N. Iran.
16. *connexa*—N.W. Iran.
16. *sahendi*—N.W. Iran, N.E. Asia Minor.
16. *elbrusensis*—N. Iran.
16. *frigida*—central Asia Minor.

The third group contains all the rest of the species in the genus. These are obviously derived species which have developed while en route or in their present areas from species that arrived earlier. The more primitive species in this group, corresponding to the less primitive ones in the preceding groups, are shown in roman type; the more advanced species are printed in italics; and the very widespread species are indicated by bold-face type.

GROUP 3

8. *Schultzii*—Abyssinia.
8. *carbonaria*—Abyssinia and Mt. Kilimanjaro.
8. *Ellenbeckii*—Abyssinia, Kenya, N. Tanganyika.
8. *hypochaeridea*—E. half of South Africa.
8. *chirindica*—Mt. Chirinda (Rhodesia).
8. *congoensis*—Elisabethville (Belgian Congo).
8. *caudicalis*—Cameroon Mts.
8. *Newii*—Tropical Africa from E. escarpment to Angola and Nigeria.
8. *scoposa*—S.W. Kenya, N.E. Tanganyika, E. Congo.
8. *glandulosissima*—Kenya Province.
8. *ugandensis*—Mt. Portal (Uganda).

8. *Swynnertonii*—N. Rhodesia, N.E. Belgian Congo.
 8. *simulans*—Melsetter district (S. Rhodesia).
 8. *Gossweileri*—Cului (Angola).
 8. *Friesii*—Ruanda (Belgian Congo).
 8. *Mildbraedii*—Belgian Congo, Uganda.
 8. *Bruceae*—Uluguru Mts. (Tanganyika).
 9. *suberostris*—E. Algeria.
 16. *purpurea*—Crimea.
 19. *palaestina*—Syria, Palestine, Cyprus.
 19. *pulchra*—Mediterranean region, Mid. Europe, E. to Himalaya and Tien Shan.
 19. *amanica*—N. Syria.
 19. *Stojanovi*—S.E. Bulgaria.
 19. *pterothecoides*—S. Syria.
 20. *alpina*—N.W. Iran, Transcaucasia, S. Russia, Asia Minor, Syria.
 20. *syriaca*—Syria, N. Palestine.
 20. *rubra*—Asia Minor, Thrace, Greece, Albania, S. Italy.
 20. *foetida*—W. Iran, Asia Minor, Syria, Mid. and S. Europe to Caspian Sea.
 20. *Schimperi*—Abyssinia.
 20. *eritreensis*—Eritrea.
 20. *Thomsonii*—N.W. India, Afghanistan, Baluchistan.
 20. *Kotschyana*—Turkestan to Caspian Sea, Iran, Iraq, E. Syria.
 20. *tybakiensis*—S. Crete.
 22. *sancta*—Mediterranean region, and E. to N. India, Turkestan.
 23. *Dioscoridis*—Greece.
 23. *multiflora*—W. Asia Minor, Scarpanto, Crete, Aegean Archipelago, E. Greece.
 23. *Zacintha*—Mediterranean region.
 24. *capillaris*—Balkan Peninsula, Crimea-Lithuania to W. Europe.
 24. *parviflora*—N. Iran, Caucasus, Asia Minor, E. Mediterranean.
 24. *insignis*—W. Syria.
 24. *neglecta*—N.W. Asia Minor, S. Bulgaria, N. Greece and W. to N. Italy.
 24. *corymbosa*—W. Greece, S. Italy.
 24. *fuliginosa*—S. Greece, E. Thessaly.
 24. *cretica*—Crete.
 24. *apula*—S. Italy.
 24. *Suffreniana*—N.W. Italy, S. France.
 25. *Noronhaea*—Porto Santo Island (Madeira Archipelago)
 25. *Balliana*—Casablanca (Morocco).
 25. *libyca*—N.W. Egypt, N. Libia.
 25. *Claryi*—Sahara Atlas (S. Algeria).
 25. *vesicaria*—Mediterranean region W. from Greece and Crete, W. Europe.
 25. *Marschallii*—Caspian region, Caucasus, Crimea.
 26. *aculeata*—Egypt, Palestine, Syria, Cyprus.
 26. *amplexifolia*—Tripolitania, Tunisia, E. Algeria.
 26. *atheniensis*—Greece.
 26. *aspera*—N.E. Egypt and N.W. Arabia to N. Syria, Cyprus.
 26. *setosa*—Caucasus, Asia Minor, Crimea, S. Europe to E. Spain.
 26. *Muhlissi*—N.W. Asia Minor.
 27. *Eueppellii*—Eritrea, Abyssinia, Kenya, Uganda, W. Sudan.
 27. *Forskali*—Yemen Province, Arabia (opposite Eritrea).
 27. *bellidifolia*—N.W. Italy, Tuscan Archipelago, Corsica, Sardinia.
 27. *burnifolia*—Italy, Sicily; and adventive elsewhere (lawn weed).
 27. *nigricans*—N. Egypt to S. Tunisia.
 27. *filiformis*—Libia.
 27. *seneciooides*—Palestine, Sinai Peninsula, Egypt W. to S. Tunisia.

In this last group it is noteworthy that, even though almost all of the species must be considered as more advanced than other species in the genus, yet only twelve, or less than 20 per cent, are very "aggressive," widespread species. And, as might be expected, practically all of these dominant species are also polymorphic, with

well-marked geographic races or subspecies. Thus, it appears that the more advanced stages of evolution in this genus have resulted in increased speciation accompanied by special adaptation to particular sets of environmental conditions. In other words, most of these more advanced species are comparatively young endemics. Only a few have combined wide adaptability with marked specialization. It seems reasonable to associate this outcome with the evolutionary history of the group, for these species certainly developed in the Turano-Iranian-east Mediterranean region during late Pliocene and Pleistocene when great topographic and climate changes took place. In all the sections represented here, except sections 22 and 27, the species in this list are connected with more primitive allies which appear in earlier lists. *Crepis sancta* (sec. 22) appears to be related to both section 16 and section 21. Section 27 may be related to *C. tenerrima*, *C. xylorrhiza*, and *C. abyssinica* of section 11. If this is true, *C. bellidifolia* and *C. bursifolia* probably migrated from north Africa across the Tunisian-Italian land bridge before the climate of north Africa reached its extreme stage of Pleistocene desiccation.

THE BASIS OF EVOLUTION IN *CREPIS*

The evidence from comparative morphology, from the chromosomes, and from interspecific hybrids, as well as from geographic distribution, points definitely to the conclusion that *Crepis* is a monophyletic group of species. Excepting sections 12 and 18 and such problematical species as *C. paludosa* and \times *C. Perssonii*, the genus as a whole is not the product of intergeneric hybridization, but rather of progressive development, from a single ancestral group, of more and more advanced and specialized types. Progressive changes, morphological, physiological, and cytological, have accompanied adaptation to changing environment caused by secular changes in topography and climate and by decimation and migration. Adaptation to changing environment has been made possible primarily by the occurrence of genetic changes, both gene mutations and grosser chromosomal changes. The course of events subsequent to the occurrence of such genetic changes depended, of course, on the conditions existing in a given population. Under certain conditions natural selection must have operated in the establishment of such dominant types as the widespread xerophytic annual species like *C. parviflora* and *C. senecioides*. Under other conditions random fixation probably served to establish local endemic types, both primitive and advanced. In all, presumably, a definite balance existed between the forces of mutation pressure, selection pressure, rate of migration, and the effects of the natural method of sexual reproduction, whether largely by self- or cross-fertilization (cf. Dobzhansky, 1941, pp. 331-344).

From a synthesis of the evidence on comparative morphology, karyology, and the cytogenetics of interspecific hybrids, it has been possible to reach some definite conclusions concerning the nature of the genetic processes which have made possible the evolution of *Crepis*. Although these have been briefly discussed in chapter 1, we here set down a summary of the conclusions reached.

- 1) The primary genetic processes causing evolution in *Crepis* are gene mutations (see p. 12) and certain structural changes in the chromosomes.
- 2) The roles of gene mutations are the production of morphological and physiological differentiation within and between species, the accumulation of intra- and interspecific sterility, and possibly the reduction in absolute size of the chromosomes.
- 3) The roles of evolutionary chromosome changes are the genesis of intraspecific sterility leading to discontinuity and hence to speciation, and of karyotype evolution through reduction in number and symmetry of the chromosomes.

4) The secondary genetic processes involved in the evolution of *Crepis* are interspecific hybridization, polyploidy, and apomixis.

5) The roles of interspecific hybridization are the augmentation of karyotype evolution and the origin of a small number of new species, especially through amphidiploidy (see Part II, sec. 15, pp. 572-616).

6) The roles of polyploidy and apomixis are a small amount of speciation, combined with extensive differentiation and geographic distribution (see especially Part II, sec. 10, pp. 416, 420; sec. 15, p. 572; and sec. 18, p. 634).

One of the most significant results of evolution in *Crepis* is the 6-5-4-3 series of haploid chromosome numbers. In this series most of the species are represented. It has been shown (Babcock and Jenkins, 1943) that all the evidence is consistent with the hypothesis that the main trend in chromosome number in *Crepis* has been a progressive decrease from a basic number of 6 to one of 3 and that this decrease took place in steps, by the loss of one chromosome at a time. Each step in decrease occurred independently of other steps and on several different occasions. It has been demonstrated in one instance (Tobgy, 1943) that the decrease from 4 chromosome pairs in *C. neglecta* to 3 pairs in *C. fuliginosa* was made possible by an unequal reciprocal translocation such that one chromosome of *C. neglecta* (or the common parent) lost nearly all of its long arm. The chromatin attached to the remaining centromere and the centromere itself are not present in *C. fuliginosa*, presumably having been lost. The loss of a chromosome, however, might also have resulted from intraspecific hybridization between two strains having translocations involving different arms of the same chromosome, namely, the one eventually lost, followed by elimination of the centromere having attached duplicated material. In either event the basic genetic process responsible for the progressive decrease from 6 to 3 pairs of chromosomes in *Crepis* is reciprocal translocation of unequal segments between nonhomologous chromosomes of individual species.

It was shown in chapter 7 that fifty-two diploid endemic species include the whole range from 6 to 3 pairs of chromosomes. The 6-paired endemics are all either primitive or intermediate in phylogenetic relations; the 5-paired ones are about equally divided among primitive, intermediate, and advanced; whereas the 4-paired species are mostly intermediate and advanced. The one 3-paired endemic (*C. fuliginosa*) is an advanced annual species. Thus, definite positive correlation exists between decrease in chromosome number and phylogenetic advancement among the endemic species, and this holds true of the diploid species in general.

That progressive reduction of chromosome numbers has been of fundamental importance in the evolution of this genus is also shown by: (1) the fact that the two species of the putative ancestral genus, *Dubyaea*, thus far examined, have a higher number ($n=8$); (2) the fact that each successive step in reduction of chromosome numbers from 6 to 3 must have occurred independently in several different species; and (3) the fact that at present the 4-paired species greatly predominate.

The antiquity of *Crepis* and the strong evidence of gradual phyletic advancement throughout the history of the genus suggest that each step in reduction of chromosome number may have required considerable time for its completion. It is possible, however, that there is some selective advantage in the lower number itself. Mather (1941) suggested that linkage of genes, in acting as a deterrent to free recombination of multiple genes, permits most of the individuals of a population to have the optimum combination of multiple genes without eliminating the reserve of variability which may be called upon when environmental conditions change.

By decreasing the number of linkage groups there is less opportunity for the occurrence of extreme variants and the consequent elimination of the genes determining them. These genes may be of great value to the plant under changed environmental conditions. In other words, linkage will tend to suppress extreme variants without decreasing the potential variability; and the fewer the number of linkage groups, the greater will be the suppression of these extreme variants.

However fundamental may have been this progressive reduction in chromosome numbers and the mechanical processes of chromosome alteration which made it possible, it should be remembered that these comprise only one phase of the whole process of evolution. Of equal or even greater importance is the role of gene mutations in speciation within groups having the same chromosome number (cf. frontispiece). Proof of this is found in the fact that the reduction from 5 to 4 pairs of chromosomes must have occurred at least four times in the history of the genus (see p. 69; secs. 4, 11, 14; secs. 13, 19; secs. 6, 8, 10, 23-27; and sec. 20). But these groups include at least fifty-eight and probably many more 4-paired species. This present diversity of species having the same chromosome number has come about largely through the origin and accumulation of gene mutations. The evidence from *Crepis* that gene mutations have been of primary importance in the differentiation of species has been reviewed in chapter 1 (pp. 14 and 16-20). It is only necessary to add that, whereas gene mutation is the basic type of genetic change involved in the differentiation of species having the same chromosome number, yet the gradual multiplication of species through the origin of gene mutations is a very complicated process. In the first place it is possible only when some kind of isolation exists between the differentiating populations. Furthermore, as was stated above (p. 145), the process continues only when a certain balance is maintained between various agencies or forces.

Isolation has certainly played an important role in *Crepis* speciation. Isolation capable of leading to speciation may be caused by (1) *spatial separation* or (2) *an internal mechanism*. With reference to the first category, migration of a species may be followed eventually by topographic changes which separate the original population into two or more populations. The spatial separation may remain merely geographic, or changes in the environment affecting the different populations may bring about the gradual accumulation of gene mutations causing physiological differences and thus establishing ecological isolation between them. Regarding internal mechanisms, effective isolation may be set up between certain individuals of the same population by the origin of genetic relations preventing reproduction or causing the sterility of the progeny of the two types of individuals. The various kinds of internal isolating mechanisms are classified and discussed by Dobzhansky (1941). The relative importance of these two categories of isolation in the development of new species in this group of plants cannot be summarily stated, too little being known as yet about the genetic relations between many of the species. But it is obvious that the kind of isolation which initiated speciation must have differed in different subgroups.

Whenever there was a decrease in chromosome number, effective genetic isolation was then established between the forms with unlike numbers. But this does not mean, as some authors imply, that speciation is "instantaneous." As stated above, the process of reducing the chromosome number may require considerable time. Furthermore, establishment of the new reduced chromosome number probably was not accompanied by much morphological or physiological change. It only made possible the accumulation of gene mutations which gradually built up morphological and physiological differentiation and added further genetic isolation to

that initiated by the change in chromosome number. Eventual migration or radical topographic changes have sometimes established geographic isolation among the species comprising a subgroup of closely related species.

An excellent illustration of the interaction of various factors in the evolution of a small group is found in the three very closely related species, *C. neglecta* ($n = 4$), *C. fuliginosa* ($n = 3$), and *C. cretica* ($n = 4$). It has been shown (Tobgy, 1943) that the second was derived from the first, or that the two species came from a common ancestor, primarily by reduction in chromosome number. At present *C. cretica* is morphologically very close to the other two species, but it is isolated geographically and its karyotype is distinct from that of *C. neglecta* (cf. figs. 246 and 248). For one thing, the A and D chromosomes (on extreme left and right in the figures) are definitely shorter than those of *C. neglecta*. A very plausible hypothesis concerning the phyletic relations between these three species assumes: (1) That their common 4-paired ancestor was distributed in the Balkan Peninsula in late Pliocene time. The fact that three other closely related 4-paired species, namely, *C. corymbosa*, *C. apula*, and *C. Suffreniana*, are now distributed from western Greece to southern France greatly strengthens this assumption. (2) That the earlier steps in chromosomal transformation, which resulted eventually in the 3-paired *C. fuliginosa*, probably occurred not later than early Pleistocene when Crete was still connected with the Balkan Peninsula (cf. fig. 7). These chromosome changes may have occurred in plants distributed in the now submerged region between Greece and Crete and may have been followed by southward migration of the new form destined to develop into *C. cretica*. The later submergence of this region left *C. cretica* completely isolated under increasingly arid, insular conditions, so that, through gene mutations, it has become an even more reduced species than *C. fuliginosa*. (3) That subsequent chromosomal transformations, occurring in plants restricted to southern Greece, produced the 3-paired form destined to develop, through accumulation of gene mutations, into *C. fuliginosa*. (4) That the remnant of the parental 4-paired species developed into *C. neglecta*, which is now distributed from northwestern Asia Minor through the northern Balkan Peninsula to Italy. Since all of these assumptions are consistent with the evidence from present-day distribution, comparative morphology, cytogenetics, and paleogeography, we may conclude that in this small group speciation was initiated by chromosomal transformations which led eventually to reduction in chromosome number and that the process of differentiation was augmented by the accumulation of gene mutations under the influence of migration, geographic isolation, and natural selection.

What has thus been shown to have been the probable history of one small group of species probably occurred over and over again in this genus. This follows from the conclusion, which was reached above, that the progressive decrease in basic chromosome numbers from 6 to 3 took place in steps, by the loss of one chromosome at a time, and by each step occurring independently on several different occasions.

It should be emphasized that chromosomal transformation is not the only genetic process leading to an internal mechanism causing isolation between species of *Crepis*. The investigations of a group of insular endemics and of a group of closely related widespread species (see pp. 17-18) produced evidence that gene mutations also bring about genetic isolation between closely related species which were already geographically isolated. Gene mutations have doubtless been continually at work throughout the history of this genus providing the genetic variations which made interspecific differentiation possible. But, in order that gene mutations could gradually build up effective genetic isolation, some other kind of isolation, partial at least, had to be initiated through either chromosomal transformation or migra-

tion into new environments or local environmental changes within the range of the species. In other words, gene mutation alone cannot ordinarily produce isolation between subdivisions of a species population under uniform environmental conditions if the population is either continuously distributed and sufficiently large or is subdivided into sufficiently large "islands" (Wright, 1943, p. 137). But, according to Wright (*loc. cit.*) : "Even under uniform environmental conditions, random differentiation tends to create different adaptive trends in different regions and a process of intergroup selection, based on gene systems as wholes, that presents the most favorable conditions for adaptive advance of the species."

There are, however, occasional extraordinary single gene mutations which act directly in isolating species genetically. The most outstanding example in *Crepis* is the interspecific lethal gene in *C. tectorum* (see p. 14). Its discovery came from the first attempts to artificially produce hybrids of *Crepis* (Babcock and Collins, 1920; Hollingshead, 1930a). The possibility that this same gene was effective in isolating *C. tectorum* from its two closest relatives, *C. Bungei* and *C. ircutensis*, has been mentioned (see p. 14). Some evidence that similar interspecific lethals exist in other species has been noted (Hollingshead, *loc. cit.*; Babcock, 1942).

Geographic and ecologic isolation, resulting from migration, also must have played an important role in *Crepis* speciation. The importance of geographic isolation is strongly indicated by the following facts concerning the present distribution of many species, facts which may be verified from the sectional distribution maps in Part II. Of the 196 species, 75, which are found in seventeen different sections or subsections, are at present geographically isolated from all of the other species in their respective groups. These groups and the number of isolated species in each are as follows: section 4, three isolated species; 5, four; 7, three; 8A, five; 8B, five; 9, three; 10C, four; 10D, three; 10E, nine; 10F, four; 11, twelve; 13, one; 16, five; 18, one; 20, two; 21, two; 23, one; 24, one; 25, four; 26, one; 27, two. Reciprocally, there are 107 comparable species which are not completely isolated geographically, that is, species the areas of which overlap or are included within the areas of one or more of their closest relatives. This makes a total of 182 comparable species. The other 14 species consist of the 4 comprising the four monotypic sections together with the 10 American species with the basic chromosome number $x = 11$. The latter consist for the most part of polyploid complexes which make them hardly comparable with most of the species in the genus.

We find that 41 per cent of the comparable species in the genus are at present geographically isolated from their closest relatives and that 59 per cent have areas that overlap those of their closest relatives. Several sections, however, have sub-groups of 2, 3, or more species the areas of which more or less overlap, but which are isolated as a group from the other species in the section. Hence the distribution maps in Part II indicate that geographic isolation has been an important factor in speciation (see, for example, figs. 131 and 184).

Although it is not nearly so apparent, it is very probable that ecologic isolation brought about through migration, either vertical or horizontal or both, into new environments has been equally important in inducing speciation. Evidence for this generalization will be found in the discussion of certain species in Part II, sections 1-6, 8, 11, 14, 19, 20, 23-25, and 27. More easily available is the evidence on endemic species (see table 8) in which 133 species are classified according to their altitude and general moisture requirements. If the present account of the history of development and migration in this genus is approximately true, it follows that ecologic isolation and accompanying specialization must have been another very important factor in *Crepis* speciation.

That there is a factual basis for the foregoing generalization becomes clear when one considers the evidence on a particular group of sympatric species (those occupying the same area). In section 19 it will be seen from figure 189 that *C. Reuteriana*, *C. palaestina*, and *C. pterothecoides* are restricted to the Syria-Palestine region and that the widespread species *C. pulchra* also occurs there. The first species mentioned is instructive in itself, since there are two well-marked subspecies. *C. Reuteriana typica* occurs at elevations from 100 to 1,900 meters and *C. Reuteriana Eigiana*, from 700 to 2,890 meters. In the mountains of Liban, where the two subspecies overlap, fertile intermediate variants occur. Evidently, subsp. *Eigiana* is much more tolerant of high altitude conditions than is subsp. *typica*; and, apparently, the overlapping areas are relatively small, although more field work is needed to establish that point. At any rate, there is partial ecologic isolation of the two subspecies, and this in course of time may become either more or less effective in differentiating the subspecies into species.

C. Reuteriana and *C. palaestina* have both been collected in the Ehden district in Liban. Whether they occur together in other areas and whether they actually grow near one another in the Ehden district is not known; but no intermediate variants have been seen by me. Hybridization experiments between these two species have not been made. It is not unlikely, however, that F_1 hybrids are fully as sterile as hybrids between *C. Reuteriana* and *C. pulchra* (see below). If this is true, their isolation in nature is due to an internal mechanism.

C. pulchra, according to the descriptions given in floras, has been reported from the Liban region in the form of subsp. *typica*. If it comes in contact with *C. Reuteriana*, it would probably be with subsp. *typica*. First generation hybrids between *C. Reuteriana typica* and *C. pulchra typica* were only 3 or 4 per cent fertile. Hence, they are well isolated by an internal mechanism. On the other hand, F_1 hybrids between *C. pulchra typica* and *C. palaestina* are 30 to 50 per cent fertile, and the F_2 progeny are vigorous and more or less fertile. So far as is known, however, the two species do not hybridize in nature. Apparently, they either do not occur together or, if they do, they do not flower at the same time. Also, *C. pulchra* is definitely a xerophyte, whereas *C. palaestina* is much more mesophytic. Finally, *C. pulchra* enters only the northern part of the area occupied by *C. palaestina*, and in the overlapping region they are apparently isolated ecologically, although difference in season of flowering may be an important factor.

C. pulchra is also genetically close to *C. pterothecoides*. Although controlled hybrids have not been made, the two species were found to have crossed in the greenhouse and the hybrids were highly fertile. *C. pterothecoides* is an even more strongly xerophytic species than *C. pulchra* and is correspondingly more advanced or specialized morphologically and physiologically. Since *C. pulchra* occurs sporadically in central Syria, it is possible that plants of the two species might sometimes occur together. But natural hybrids would be very unlikely to occur because *C. pterothecoides* is very precocious in time of flowering and, under desert conditions, the flowering period would be short, whereas *C. pulchra* is slow in developing to the flowering stage. This marked physiological difference would serve as an effective isolating mechanism.

The above illustration serves to emphasize the complicated nature of the isolating factors which separate closely related sympatric natural species. Our present knowledge of this genus is too incomplete to make possible a more definite statement concerning the nature of the isolation of other sympatric species of *Crepis*. But the known or strongly indicated relations between the members of this one group will serve at least to indicate the nature of the isolating factors in other groups of closely

related species the areas of which more or less overlap one another. It is certain that ecological specialization has played an important role; but other kinds of genetic differentiation, such as difference in flowering season, have also been important.

Stebbins (1942b), in discussing the role of isolation in the differentiation of plant species, has advanced the hypothesis that internal isolating mechanisms evolve gradually and are genetically independent of the morphological changes which produce visibly different species. Clausen, Keck, and Hiesey (1945) also emphasize the *gradual* development of such isolating mechanisms. Although supporting experimental evidence is not available in *Crepis*, the history of the genus, as recorded in this monograph, cannot fail to give the impression that the evolution of this group has been a slow, gradual process.

The tempo of evolution, however, has not been uniform among the species comprising this genus. In fact, the general picture resembles that portrayed for the Carnivora and the Pelecypoda by Simpson (1944, p. 128) in that only a few of the existing species of *Crepis* can be considered to have originated in early Tertiary, whereas a large proportion of them must have had their origin during Pliocene-Pleistocene (see pp. 139-141). Thus, the evidence from *Crepis* indicates that this genus includes at least two types of species with reference to their tempo of evolution: (1) the few most primitive species in the genus which have changed very little since early Tertiary; and (2) the many more advanced intermediate species and the most advanced species, all of which have probably evolved since mid-Pliocene.

The extreme contrasts between oldest and youngest species in this genus (for example, *C. sibirica* and *C. suberostris* or *C. conyzaeifolia* and *C. seneciooides*) can be harmonized by the conception that the extremes are actually connected by extensive series of intermediate types. Many of these intermediate species still exist, but many others have doubtless become extinct. A large proportion of those which still exist are endemic relics which occur in restricted areas presumably because of their definitely limited tolerance to environmental variations. Most of the youngest species in the genus are also endemics which appear to be restricted in distribution because, along with their specialization, they have become adapted to particular sets of environmental conditions; whereas only a dozen or so combine high specialization and wide adaptability (see p. 144).

In general, adaptation in *Crepis* involves physiological changes which are correlated with progressive morphological changes and reduction in chromosome number. The most important adaptive trend in the genus includes those changes which accompanied the persistence of old species and speciation under increasingly xeric conditions. Outstanding among these changes are: (1) development of the deep taproot from the rhizome; (2) development of the biennial, the annual, and the precocious annual from the perennial life cycle; (3) reduction in size of the plant and its parts; (4) increased specialization for seed distribution by the wind, including increase in number and reduction in size of the flower heads, thickening and reflexing of the inner involucral bracts, decrease in size and weight of achenes, and development of a slender beak on the achenes; and (5) increase in length of viability of the seeds, as in *C. capillaris* and *C. seneciooides*.

Certain species of *Crepis* have also developed various special adaptations. For example, the most characteristic change accompanying adaptation to high alpine conditions is development of the low, tufted habit of the plant (*C. terglouensis*, *C. nana*). The ability of *Crepis pygmaea* and *C. nana* to colonize steep, gravelly slopes resulted from the development of stolonlike underground shoots. In *Crepis patula* and *C. Zacintha* extreme induration of the involucres results in enclosing the achenes until the involucre disintegrates. In the last two species this particular

modification may make possible the distribution of the seeds by streams. In *Crepis Clausonis* and *C. vesicaria* subsp. *hyemalis*, the strictly winter-blooming habit seems to be a special adaptation to seasonal moisture.

Regardless of any doubts concerning the validity of the special adaptations listed above, the general importance of the morphological and physiological changes

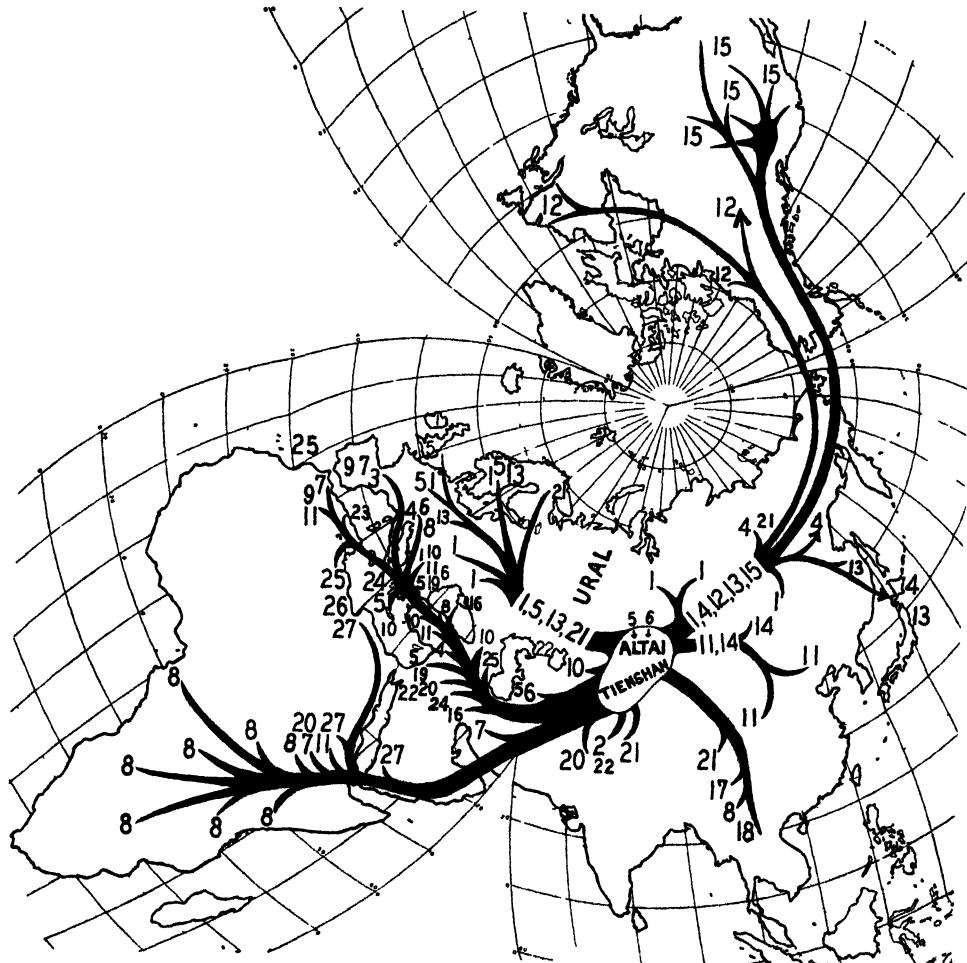


Fig. 11. Diagrammatic representation of the principal migration routes of *Crepis* from the assumed center of origin in Central Asia. The numbers designate the sections. From the Altai region, sections 1, 5, 13, and 21 moved westward, and sections 1, 4, 11, 12, 13, 14, 15, and 21 moved northeastward and eastward. From the Tien Shan region, sections 8 (one species), 17, 18, and 21 moved southeastward, and all the other sections or their progenitors moved southward and southwestward. Based on Goode Base Map No. 201 PC. By permission of the University of Chicago Press.

that have accompanied adaptation to an increasing desiccation of the climate cannot be doubted. All of these adaptations appear to have developed gradually through the accumulation of minor genetic changes.

The evolution of *Crepis* has depended primarily upon two general categories of genetic change: (1) gene mutations and (2) reciprocal translocations between nonhomologous chromosomes. But the evolution of *Crepis* has involved adaptations

to almost every type of environmental change to which flowering plants have been subjected throughout their long development. These adaptations have come about, presumably, not only through natural selection but, in some species, through limitation of population size, which has resulted in random fixation or genetic drift (gene spread). The forces of natural selection, random fixation, and gene spread have been brought into play partly through the migration of species into new environments and partly through secular or catastrophic changes in topography and climate. Spatial isolation of populations, resulting from any of the above conditions, has been of paramount importance in the development of new species. And the reuniting of more or less differentiated populations through migration has apparently been important in developing such polymorphic superspecies as *C. foetida* and *C. vesicaria*. Genetic isolation, induced by such an internal mechanism as that set up by the process leading to reduction in chromosome number, has also played an important role in *Crepis* speciation. But equally important in the multiplication of species with the same chromosome number is the differentiation, both morphological and physiological and including other internal isolating mechanisms, which has been brought about through the gradual accumulation of gene mutations. The development of those other internal isolating mechanisms, such as difference in flowering season and genetic incompatibility or hybrid sterility due to genic divergence, probably depended on some kind of spatial isolation for the conditions essential for their development (see Dobzhansky, 1941, pp. 280–288).

The results of evolution in this genus are epitomized by the contrast between the oldest and youngest species. The most primitive *Crepis* species are robust, rhizomatous, mesophytic perennials with large simple fruits and short-lived seeds. The highest culmination of the long history of the group is found in the small, delicate desert annuals, with their extreme precocity, ephemeral fibrous taproot, tiny fruits with a filamentous beak, and seeds of longer viability.

It may be well, in conclusion, to repeat that the basis of taxonomic classification in this work consists of morphological and chromosomal resemblances and differences, supplemented by evidence from ecology, genetics, and cytogenetics. Along with this evidence, it was possible to use the evidence from geographic distribution in constructing a hypothetical scheme of phylogenetic relations between the sections, and between *Crepis* and its putative ancestors, which was found to be consistent with the limited fossil record of *Crepis* and with a great mass of paleobotanical and floristic evidence on the development and migration of floras in Eurasia, North America, and Africa. The consistency of this evidence on phylogeny and geographic distribution warrants the derivation of conclusions pertaining to evolutionary processes in *Crepis* which are of general significance.

SUMMARY

This account of the origin and migrations of *Crepis* is summarized diagrammatically in figure 11, which indicates the probable center of origin, the general direction of the four migration routes, and, roughly, the distribution of the twenty-seven sections. The center of origin and the migration routes have been assumed on the basis of the following:

- 1) Evidence from morphologic, karyologic, and genetic resemblance, indicating that the genus is essentially monophyletic.
- 2) Evidence from the present distribution of closely related genera and of the more primitive sections of *Crepis* which, considered as a whole, certainly indicates radiation from an Asiatic center along the four main migration routes assumed for *Crepis*.

3) Evidence from geology that the Altai-Tien Shan region was an available and suitable environment for the development of *Crepis* during the Tertiary period; that the great mountain axis to the south was of later origin; that the Beringian land bridge was available for the migration of the progenitors of section 15 and one species of section 12 into North America; and that the gradual desiccation of the Obic and Tethys seas during the first half of the Tertiary period, followed by gradual lowering of the temperature during the second half, provided conditions favoring the westerly and southerly trends of migration.

4) Evidence from paleobotany indicating that the Altai-Tien Shan region was part of a Tertiary floristic province in which *Crepis* could have flourished; and that many species of woody plants, including *Cedrus*, *Datiscia*, and *Fagus*, were distributed to the east, south, and west from that general region in the Tertiary period.

5) Evidence from the present distribution of many genera of plants, including some in the Crepidinae, particularly *Taraxacum*, indicating a similar history to that of *Crepis*.

6) Evidence from endemism which is of outstanding importance in this genus. More than 70 per cent of the species are endemic, including some of the most primitive and some of the most advanced species. The primitive endemics are relics, being the present-day representatives of ancestral species which were widely distributed in Miocene-Pliocene. These primitive relics of restricted distribution were able to survive the severe climatic fluctuations of the Pleistocene epoch by becoming adapted to the special niches which they now occupy. The advanced species of the Mediterranean region, including the littoral endemics, were also derived from ancestors, some of which were probably distributed from Central Asia to the shores of the Atlantic Ocean in late Pliocene and early Pleistocene. During the most severe periods of desiccation they became adapted to the special conditions existing in the regions or localities where they now occur.

7) The numerous secular changes in topography and climate which occurred throughout southern Eurasia and northern Africa, especially during the latter half of the Tertiary and the Quaternary periods, provided suitable conditions for the development of new types, especially for progressive evolution toward the annual xerophytic type. These changes also caused the restricted distribution of many species.

8) The evolution of more and more advanced types of *Crepis* species from a single ancestral group has been made possible, primarily, by the occurrence of gene mutations (see p. 12), together with such structural changes in the chromosomes as may lead to genetic isolation, and, secondarily, by interspecific hybridization, polyploidy, and apomixis.

9) Speciation in *Crepis* depends not only upon the origin of new genetic changes but also upon the occurrence of some kind of isolation which prevents the differentiating populations from interbreeding. Gene mutations are essential for differentiation, but they cannot induce speciation in the absence of some kind of isolation, either spatial isolation (geographic or ecologic) or isolation due to an internal mechanism. Chromosome alterations leading to reduction in chromosome number initiate isolation; and this type of genetic isolation is of primary importance in *Crepis*, since most of the species are diploid and they comprise a progressively reducing series of haploid chromosome numbers from 6 to 3. Gene mutations can develop a type of genetic isolation between two populations only if the populations are already isolated in some other way.

10) The new biotypes produced by fortuitous genetic changes are assumed to have been subjected to natural selection and to any of the changing genetic condi-

tions resulting from migration, from decrease and increase in size of population, and from spatial isolation and reunion of populations.

11) Adaptation to gradually increasing xeric conditions has been of special importance in the evolution of this genus. The morphological and physiological changes making this adaptation possible have been part of the general process of differentiation through gene mutations under the influence of natural selection.

APPENDIX 1

SOME CREPIS PROBLEMS CALLING FOR FURTHER RESEARCH

THE PRESENT AUTHOR is keenly aware of the numerous problems connected with the origin and evolution of the genus *Crepis* which require further research for their solution. It is his hope that by calling attention to some of them there will be a better chance of their receiving consideration on the part of other scientists, especially of botanists situated in or near those countries where the various problems can be most conveniently attacked.

INTERGENERIC RELATIONS

Crepis and *Dubyaea*.—That *Crepis* and all the other genera of subtribe Crepidiinae originated from the genus *Dubyaea* when that group was much larger and more widely distributed than it is at present seems to be a safe assumption (cf. pp. 62-65). But a gap exists in the chromosome number of *Dubyaea* and those of *Crepis*. Except for the obviously derived groups of *Crepis* (sec. 12, *Ixeridopsis* ($n = 7$), sec. 15, *Psilocheaenia* ($x = 11$), and possibly sec. 18, *Pyrimachos*, in which no chromosome studies have yet been made), the highest haploid or basic number is 6. In *Dubyaea*, on the other hand, the lowest known number is 8. It was necessary, therefore, to assume that *Dubyaea* or primitive *Crepis* species existed in the past, if not now, with the haploid number 7. In section 12, *Ixeridopsis*, it was also necessary to assume that *Crepis* species, or *Crepis*-like *Dubyaea* species, once existed with the haploid number 7 (cf. p. 65); and that these hybridized with certain *Ixeris* species, or *Ixeris*-like *Dubyaea* species, also with the number 7 (cf. p. 70).

Up to the present, only two species of *Dubyaea*, namely, *D. oligocephala* and *D. hispida*, have been examined cytologically. It would be highly desirable, therefore, that all the other known species of *Dubyaea* be obtained in living condition and be studied, cytologically at least. Hybridization experiments with all of these *Dubyaea* species and the most primitive species of *Crepis*, followed by cytogenetic research on such hybrids as could be obtained, would of course be equally desirable. The technical difficulties of rearing these primitive species are considerable, but they are probably not insurmountable, even though special techniques are likely to be required. For example, in working with high alpine species at stations situated at low elevations, it has been found advantageous to sow the seeds in flats and to transport them to higher elevations where they will be exposed to the elements during winter and spring. It is important that they be covered with snow during winter and that they be subjected to alternate freezing and thawing in the early spring. It is probable that an artificial setup simulating these natural conditions could be devised. Still more certain and satisfactory would be the culture of the plants from living roots brought to the experimental station from their natural locations. During the summer of 1930 the author himself collected living roots of nine perennial species of *Crepis* in the Mediterranean region, some of which were high alpine plants, and sent them by ordinary post (not by airplane) via Washington to California without the loss of a single species. He has never been able to obtain living roots of any Asiatic species; but with adequate preparation for their collection and preservation it should be possible at least to examine the chromosomes of these Asiatic alpine species. The desirability of thorough exploration for additional primitive *Crepis* and *Dubyaea* species in Asia is discussed below under distributional problems.

Crepis and Youngia.—The problem of the true generic status of *Youngia tenuifolia* (Willd.) Babc. et Stebbins (Carnegie Inst. Wash. Publ. No. 484: 46-59, 1937) is still somewhat in doubt. To be more precise, one should say that it is the *exact origin* of this polymorphic, polyploid, and partially apomictic complex of forms which is in doubt. Probably it is more satisfactorily disposed of by keeping it in the genus *Youngia* than by transferring it back to *Crepis*. At any rate, before restoring it to *Crepis* all angles of the problem should be very carefully considered, and efforts should be made to obtain more factual data bearing on its origin.

It was pointed out by Babcock and Stebbins (*op. cit.*, p. 59) that, in order to account for the morphological characteristics of all of the polyploid forms comprising *Y. tenuifolia*, it is necessary to assume the existence, now or earlier, of at least three different diploid ancestors. One of these assumed diploids would represent the foundation stock of subsp. *typica*, another subsp. *altaica*, and the third must have been involved in the origin of subsp. *diversifolia*. The geographic distributions of the three subspecies are as follows: *typica*, in S. Siberia from Irkutsk to Nertchinsk Provinces and south to N. Manchuria and Mongolia; *altaica*, in the S.W. Altai region; *diversifolia*, from the Altai Mts. through the mountains of Turkestan and W. Tibet to the Himalayan region. Thus two of the assumed diploids might be expected to occur in Central Asia, but diploid *typica* would probably have to be looked for farther to the east.

Babcock and Stebbins (*loc. cit.*) also state: "The phyletic relations of the diploid subspecies with other species of *Youngia* are more obscure. Too little is actually known about chromosome number and morphology in this genus to warrant any hypothesis based on cytological evidence. If the diploid subspecies of *Y. tenuifolia* are 5-paired, one could assume that they represent a connecting link between *Youngia* and *Crepis*, a hypothesis supported by their morphological characteristics."

Searching for these assumed diploid forms of *Y. tenuifolia*, therefore, is to be encouraged, not only with the object of learning more about the nature and origin of this interesting heteroploid complex (see Babcock and Stebbins, 1938, pp. 58-69), but also because such investigation may throw more light on the relationship between *Youngia* and *Crepis*. It is hoped that botanists of the U. S. S. R. will take a special interest in these problems.

Crepis and Ixeris.—The probability that section 12, *Ixeridopsis*, originated through hybridization between *Crepis* species and *Ixeris* species with $n = 7$ chromosomes, or between two *Dubyaea* species which had already become *Crepis*-like and *Ixeris*-like, was mentioned above. Cytogenetic experiments with attempted hybrids between *Ixeris alpicola* and any available species of section *Ixeridopsis* might throw some light on this interesting problem.

Crepis and Hieracium.—The possibility that *Crepis paludosa* originated through hybridization between *Crepis* and *Hieracium* before these two genera were as strongly differentiated as at present (cf. Part II, p. 236) might be investigated by cytogenetic research on hybrids between *C. paludosa* and various *Hieracium* species, for example, *H. Knuthianum* (cf. Pax, 1898, p. 32).

MORPHOGENETIC PROBLEMS

Plant form and phylogeny.—Raunkiaer (1937, p. 42) asserts that the "Proto-Hemicryptophytes pass imperceptibly into the Suffruticose Chamaephytes, from which most of them are certainly descended." All the species recognized as most primitive in *Crepis* are Hemicryptophytes. They have a rhizome and 6 pairs of chromosomes. The few suffruticose or suffruticulose species in this genus all have deeply penetrating taproot and less than 6 pairs of chromosomes. Is this actually

an exception to the generalization of Raunkiaer? Or should one after all assume that, even in *Dubyaea*, the deeply penetrating root and suffruticose habit was more primitive and that the corresponding species of *Crepis* were derived from such ancestors? This latter assumption would require the recognition of a still greater gap in chromosome numbers than now exists between *Crepis* and *Dubyaea*, unless, indeed, one of the existing species of *Dubyaea* with a taproot should turn out to have 7 or 6 pairs of chromosomes. On the basis of this assumption it would follow that the rhizomatous species of *Dubyaea* and *Crepis* are derived forms which have become adapted to a very moist habitat. Because of the evidence within *Crepis* indicating that several species characterized by a taproot were derived from rhizomatous species (for example, sec. 14 derived from sec. 4, and sec. 19 from sec. 13), my assumption that the most primitive species of *Crepis* (and probably of *Dubyaea*) were rhizomatous seems probable. But it is equally probable that the most primitive species of *Dubyaea* were taprooted. Attention is called to this problem in order to emphasize the desirability of research on the phylogenetic relations between these two types of species in both these genera; and this further emphasizes the importance of future exploration in Central Asia for additional species of both genera.

Crepis rhaetica of section 4 offers especially promising material for an ontogenetic investigation of development of the underground part of the plant. No question exists about the subcaudical part being a rhizome, since a comparison of its gross histology proves that it is closely similar to that of *C. sibirica* and *C. kashmirica*. With the help of Dr. Adriance S. Foster, pieces of rhizomes of these three species were bleached and cleared sufficiently to reveal their gross structure.¹ In *C. sibirica* and *C. kashmirica* the vascular system has the aspect of a typical dictyostele. When a piece of the rhizome is split longitudinally each piece contains a half-cylinder of yellow woody tissue. Inside the cylinder is the pearly white parenchymatous tissue of the pith, and outside of it is the cortical tissue. Every lateral root could be seen to contain a central vascular strand which branched off from the stele. The rhizome of *C. rhaetica* is closely similar to those of *C. sibirica* and *C. kashmirica*, except that the stele is not composed of so many vascular fibers, which fibers could be seen to be interlaced. Since lateral root fibers arise in the same way as in the other two species, there can thus be no question about these species being rhizomatous.

C. rhaetica, however, in that its rhizome apparently has a growing point at each end, presents a special problem, which is taken up in Part II, p. 254, and figure 24. Unfortunately, in all the herbarium material thus far examined, the lower growing point could not be demonstrated and it is assumed to have been broken off. It would certainly be of interest to grow a considerable number of seedlings of this species so as to make examinations at successive periods in ontogeny. This should establish beyond any question the method of downward elongation of the rhizome in this species. Such a study would also provide valuable evidence on the relation between the rhizome and the hypocotyl, and should answer the query whether the seedling of a rhizomatous species first produces a true root which aborts after the rhizome begins to develop. If this should be found to be the typical ontogenetic behavior in rhizomatous species, it would be an argument in favor of considering the taproot more primitive than the rhizome. All the phylogenetic evidence within *Crepis* points to the opposite conclusion, but this does not invalidate the assumption that the more distant ancestors of *Crepis* were taprooted.

Observations on the development of the root system in young seedlings of four

¹ Following are the essential steps in the process: (1) heat in water for an hour or less; (2) transfer to 5 per cent sodium hydroxide and place in oven at 52–53° C. for two or three days; (3) wash in water, dehydrate in ethyl alcohol, and examine in alcohol under the dissecting microscope.

species of *Crepis* certainly indicate that the taproot is a more primitive feature than the rhizome. The first of these species is *C. hierosolymitana*, one of the few rhizomatous species of which viable seed was available. The second of these four is *C. Reuteriana* subsp. *Eigiana*, which, from herbarium specimens, is known to develop a strong woody subterranean stem and which has therefore been considered an intermediate type between the rhizomatous and the taprooted types. The other two species are *C. scaposa* subsp. *taraxaciformis*, a perennial, and *C. pulchra*, an annual, both being taprooted. With the assistance of Mrs. Ruby Allen Valencia, seeds of these four species were germinated and cultured individually in pots under uniform conditions and studied histologically in their earlier stages of development.

C. hierosolymitana. All the seedlings developed a primary root which developed as a taproot with many branches. Cross sections of the main root taken just below the caudex showed an arrangement of xylem elements which is typical of root structure. It is clear that the rhizome must develop later in ontogeny; and apparently it develops from the caudex and is accompanied by the appearance of adventitious roots.

C. Reuteriana. The seedlings developed a primary root which continued to develop as a taproot to the end of the period of study. At that time all cross sections of the taproot showed the typical central stele characteristic of root structure. Sixteen months later (June, 1946), after these seedlings had flowered twice, it was found that the caudex was about 2 cm long, the upper half being a rhizome about 6 mm in diameter, with typical stem structure and small lateral roots; and the lower half, about twice as thick, was intermediate in structure, bearing large lateral roots and tapering into the strong taproot. Hence, it may be inferred that the underground stems, seen in certain herbarium specimens, developed by annual increments about 1 cm in length and that such specimens must be at least 9 or 10 years old. It is evident that, in this species, the caudex begins to develop as a rhizome in the second year. The strong roots at the base of the caudex are adequate to support the plant for years, and the small lateral roots of the rhizome may disappear completely, giving it the appearance of an underground stem.

C. scaposa and *C. pulchra*. As was to be expected, seedlings of both of these species developed a taproot which continued to grow throughout the period of study.

The evidence is clear that the hypocotyl develops into a root in all four species. For this reason the root must be considered a more primitive structure than the rhizome. This is consistent with the hypothesis that the rhizome is merely a modified caudex with adventitious roots and that it was evolved as an adaptation of a taprooted type to a moist environment.

The genetic basis of root versus rhizome.—This is another phase of the foregoing general problem which the present author has not been able to study in the progeny of interspecific crosses. It is very desirable that this be done. But it is practically essential that such work be attempted at a station where the wild species themselves will thrive and develop their characteristic subterranean parts. This probably calls for garden cultures under conditions simulating as nearly as possible the natural habitats of the wild species. In this connection there should also be conducted some transplantation experiments from the natural habitats to conditions less and less natural for each species in order to ascertain the degree of direct modifiability in type of root which is latent within each species.

The genetic basis of beaked achenes.—Such crosses as have been made between species of *Crepis* with beaked and unbeaked achenes indicate that the beak is the result of the accumulation of numerous minor mutations. It is very desirable, however, that this question be investigated further by first finding two species,

one with long beaked and the other with shortly beaked or unbeaked fruits, which will produce hybrids with sufficient fertility to make possible a large-sized second generation.

DISTRIBUTIONAL PROBLEMS

The need of exploration for additional species.—That *Dubyaea* species may exist in Central Asia is an interesting possibility. The fact that one species of *Soroseris* is known from Tien Shan seems to increase the likelihood of such a discovery. Furthermore, a 7-paired *Dubyaea* would strengthen our hypothesis about the origin of *Crepis* (see p. 65). It is hoped that botanical collectors will keep this desideratum in mind. Search should also be made, probably in the eastern Tien Shan and Dzungaria regions or perhaps also in eastern Altai, for the diploid forms of *Youngia tenuifolia*. The possibility that other species of *Ixeris* than *I. alpicola* were involved in the origin of section 12, *Ixeridopsis*, and that such species of *Ixeris* may still exist in Central Asia should be kept in mind. The possibility also exists that primitive, relic, alpine species of *Hieracium*, having close relatives in Europe, may yet be found in Central Asia. That such species are completely absent from that region, as well as from the arctic regions and from Scandinavia, was accepted by Engler (1879, p. 131) as evidence that the alpine *Hieracia* of southern Europe (Pyrenees, Alps, Carpathians, Balkan Peninsula) developed since the glaciation of Europe. But this does not preclude the possibility that their ancestors migrated from Central Asia into southern Europe over the same southwesterly route that *Crepis* followed. Engler finds it necessary to assume that *Hieracium alpinum* existed during the Glacial epoch and was able to migrate from the Alps to Sudeten, Harz, Scandinavia, Karisch Gulf, Greenland, and other parts of arctic America. But most of these alpine *Hieracia* are assumed to have arrived from Central Asia too late to be able to cross the European lowland to the north of the Alps. If they or their ancestors actually did migrate from Central Asia, it would seem likely that sooner or later some traces of these relics would be discovered along the route or in the assumed region of origin.

Distribution in Crepis Dioscoridis.—An interesting distributional problem is presented in connection with the question concerning the real nature of the forms recognized as subspecies (cf. Part II, pp. 746–757). Three of the four subspecies of *Crepis Dioscoridis* are known from very scanty material and each from only a single locality. Thorough field studies are needed and should be supplemented by garden cultures designed to test the amount of natural hybridization going on. Since all three of these subspecies occur within the geographic area of subsp. *typica*, it would seem that they may be isolated from the latter, to some extent at least, either ecologically, seasonally, or by internal mechanisms.

Distribution in Crepis neglecta.—Similar problems exist with respect to *Crepis neglecta* and some of the species most closely related to it. Although it is known that an effective isolating mechanism exists with respect to *C. fuliginosa* of southern Greece and eastern Thessaly, it would be desirable to ascertain the exact southern limits of *C. neglecta* in Greece and the amount of intergradation between the two species along this boundary. The relation between *C. corymbosa* and *C. fuliginosa* is similar, since the two may meet in northwestern Greece or the adjacent islands. Whether *C. corymbosa* and *C. neglecta* contact each other is not known, but it is certain that *C. corymbosa* occurs in the area of southern Italy occupied by *C. apula*, where the two species seem to be well isolated by their different flowering seasons. *Crepis neglecta* also occurs in southern Italy, but it may be isolated from *C. apula* in the same way. Additional investigations on these species and the relationships between them are certainly desirable.

Distribution of the subspecies of Crepis albida.—Another problem worthy of thorough investigation is that concerning the distribution and degree of isolation of the several subspecies of *Crepis albida*. Although several have previously been recognized as species, yet some evidence of intergradation exists, at least between a few of them; furthermore, *C. albida Grosii* is an extremely variable complex of forms. Two of these subspecies have been found to grow well and to produce abundant seed in the experimental garden. It is very desirable that they all be brought together for comparison, experimental crossing, and cytological study, and that adequate field studies be made of their distribution and variation.

A number of other *Crepis* species need investigation concerning the actual nature of their subspecific forms, both distributionally and genetically. Among these may be mentioned especially: *C. sibirica*, *C. paludosa*, *C. pygmaea*, *C. aurea*, *C. conyzae-folia*, *C. achyrophoroides*, *C. aurea*, *C. hypochaeridea*, *C. Newii*, *C. scaposa*, *C. suberostris*, *C. biennis*, *C. bupleurifolia*, *C. oreades*, *C. heterotricha*, *C. armena*, *C. Reuteriana*, *C. palaestina*, *C. pulchra*, *C. Bodinieri*, *C. rigescens*, *C. lignea*, *C. alpina*, *C. foetida*, *C. sancta*, *C. capillaris*, *C. Bourgeauii*, *C. vesicaria*, *C. aspera*, *C. setosa*, and *C. Rueppellii*. Also, several species known only from the type locality deserve special attention with respect to their present size and distribution. Arranged by regions, these are: Balkan Peninsula and Crete: *C. Guioliana*, *C. Schachtii*, *C. tybakiensis*, and *C. Atheniensis*. Asia Minor and Syria: *C. albiflora*, *C. khorassanica*, *C. amanica*, *C. insignis*, and *C. Muhlisi*. Central Asia and Iran: *C. darvasica* and *C. demavendi*. Southeastern Asia: *C. chlorooclada*. Africa, northern: *C. Faureliana*, *C. Fontiana*, *C. Balliana*, and *C. Claryi*. Africa, tropical and southern: *C. suffruticosa*, *C. urundica*, *C. chirindica*, *C. congoensis*, *C. ugandensis*, *C. simulans*, *C. Gossweileri*, *C. Friesii*, and *C. Bruceae*.

The species which have not yet been investigated cytologically or genetically but which, in order to round out the evidence from the chromosomes as well as geographic distribution, should at least have their chromosomes examined, listed by sections, are: (4) *C. dioritica*. (5) *C. smyrnaea*. (6) *C. rhaetica*. (7) *C. achyrophoroides* and *C. elymaitica*. (8) *C. keniensis*, *C. iringensis*, *C. meruensis*, *C. cameroonica*, *C. Schultzii*, *C. carbonaria*, *C. Ellenbeckii*, *C. urundica*, *C. chirindica*, *C. congoensis*, *C. caudicalis*, *C. glandulosissima*, *C. ugandensis*, *C. Swynnertonii*, *C. subscaposa*, *C. simulans*, *C. Gossweileri*, *C. Friesii*, *C. Mildbraedii*, and *C. Bruceae*. (10) *C. Strausii*, *C. darvasica*, *C. songorica*, *C. sonchifolia*, *C. bertiscea*, *C. bupleurifolia*, *C. albanica*, *C. macropus*, *C. dens-leonis*, *C. Sibthorpiana*, *C. khorasanica*, *C. auriculaefolia*, *C. turcica*, *C. Pantocsekii*, *C. turcomanica*, *C. Guioliana*, *C. crocifolia*, and *C. athoa*. (11) *C. pinnatifida*, *C. tenerrima*, *C. xylorrhiza*, *C. Faureliana*, *C. heterotricha*, *C. armena*, *C. demavendi*, and *C. abyssinica*. (12) *C. corniculata*, *C. alaica*, *C. lactea*, and *C. naniforma*. (14) *C. ircutensis*. (16) *C. connexa*, *C. sahendi*, *C. purpurea*, *C. elbrusensis*, and *C. frigida*. (17) *C. napifera*. (18) *C. Phoenix*, *C. Bodinieri*, *C. rigescens*, *C. lignea*, and *C. chlorooclada*. (19) *C. amanica*. (20) *C. tybakiensis*. (21) *C. tibetica*, *C. Gmelini*, and *C. elongata*. (24) *C. insignis*. (25) *C. spathulata*, *C. Salzmannii*, *C. Balliana*, and *C. Claryi*. (26) *C. Atheniensis* and *C. Muhlisi*. (27) *C. Rueppellii*, *C. Forskalii*, and *C. filiformis*.

The genetic nature of narrow endemics in Crepis.—In connection with distributional problems, mention should be made of the interesting questions connected with population dynamics. These questions, of course, involve genetic relations rather than merely distributional ones; but the facts of distribution in nature certainly have a direct bearing on the nature of the population. For example, in chapter 7 (pp. 128-129) is given a brief discussion of the nature of narrow endemic species in *Crepis* which is based on those few species concerning which enough is

known to warrant the assumption that they are of very narrow distribution. Even so, for these few species and others, more definite information concerning distribution and variability is greatly to be desired. The present author believes that *Crepis* offers many attractive opportunities for profitable studies on population dynamics.

EVOLUTIONARY PROBLEMS

Interspecific lethal genes.—The first of the two generally important evolutionary problems of a genetic nature, which certainly deserve consideration from students who are planning future investigations in experimental evolution, is that concerning the generality of occurrence of interspecific lethal genes in *Crepis* and the true nature of the roles they have played in speciation. After the discovery by Hollingshead (1930a) of an interspecific lethal in *Crepis tectorum*, causing the early death of hybrids with *C. capillaris*, it was the hope of the present author that a comprehensive search for such lethals could be made among many species of *Crepis*. A systematic effort to this end has not been possible, although certain incidental data seemed to indicate that such genes may exist in other *Crepis* species. In order to make such a systematic research, a large collection of species in living condition must be accumulated and maintained for a period of years. This in itself is an expensive undertaking. Unfortunately, it has not been possible to preserve in living condition many of the species which were once under cultivation at the University of California. It will require years to build up another such collection even after war conditions are sufficiently ameliorated to allow it being done. But sometime, somewhere, such a collection should once more be brought together. Then, this research for interspecific lethals and many other genetic and cytogenetic problems can be worked out.

Meanwhile, we are faced with one particular problem of a kind which I hope some Russian geneticist will be able to solve. If the interspecific lethal in *Crepis tectorum* actually was of evolutionary significance, it should have functioned in isolating this species from its two nearest relatives, *C. Bungei* and *C. ircutensis*. Experimental hybrids between *C. tectorum* and *C. Bungei* have not been made; and *C. ircutensis* has never been brought into cultivation. It would be very desirable to bring these three species together under controlled conditions and to make experimental crosses using numerous individuals of each species for the purpose of finding different genotypes with reference to the lethal gene.

Self-incompatibility.—The second problem of general evolutionary significance is that concerning the genetic basis of self-incompatibility in *Crepis*. Although many species, like *C. tectorum* and *C. pulchra*, are highly self-fertile, many others are more or less self-sterile. This has been shown by Hughes (1943) in *Crepis foetida* subsp. *rheeadifolia* to be due to self-incompatibility of the pollen. Cytological studies have shown that a plant's own pollen usually fails to germinate, and in the rare instances when it does germinate it fails to penetrate the stigmatic surface. Among the material available, four intrsterile groups were discovered, some of which were also intersterile. From the data on three generations of crosses, we may make certain assumptions concerning the genetic basis of self-sterility in this subspecies. One major set of alleles is responsible for the self- and cross-sterilities. They are designated S_1 , S_2 , S_3 , and S_4 . It is postulated that (1) Pollen behavior is sporophytically determined. That is, the behavior of a pollen grain is dependent upon the genotype of its parental sporophyte. (2) S_1 is recessive to all three of the other alleles. S_2 is dominant to S_1 , but recessive to S_2 and S_4 ; whereas S_3 and S_4 are both dominant to the weaker alleles, but either is capable of completing the expression of the other. (3) *Reciprocal differences are due to dominance, and not, as in other*

known cases, to homozygosity of one parent. Other genes at different loci are believed to be able to exert modifying effects, especially when associated with the recessive S alleles.

It would be very desirable to have these findings checked by experiments with *C. foetida* subsp. *commutata*; and to have these results compared with the basis of self-incompatibility in other species of *Crepis*. The general role of self-incompatibility in the evolution of various *Crepis* species should eventually be worked out.

CYTOGENETIC PROBLEMS

Among the many cytogenetic problems which remain to be solved in *Crepis*, only a few can be mentioned here. These are problems which have been recognized by the author and his associates but which it has not been possible to attack.

Chromosome pairing in interspecific hybrids.—As was pointed out on page 58, it is desirable that there be a well-planned repetition, on a much larger scale, of Avery's (1930) cytological studies on chromosome pairing in interspecific hybrids having *Crepis leontodontoides* as one parent. The general significance of these and similar experiments in hybridizing species of *Crepis* has been shown (Babcock and Emsweller, 1936, p. 359) to support the conception that all species of *Crepis* had a common origin and are still more or less similar in genetic composition. But it was also pointed out (*op. cit.*, p. 355) that, in order to generalize concerning the phyletic relations of the species on the basis of comparative meiotic regularity, there should be *several series of hybrids* in each of which a single species is used as one parent of each cross. The above suggestion, that *C. leontodontoides* might be used as the common parent in one such series, is based on Miss Avery's success in crossing it with several widely separated species and more recent crosses between it and still other species. From its phylogenetic relations it seems probable that *C. Bungei* might be used successfully in another such series of hybridizations. Obviously, such investigations as these can be carried on only where a large collection of *Crepis* species, representing as many sections as possible, is maintained for research purposes.

Structural hybrids and speciation.—The bearing of structural hybrids on speciation in *Crepis* provides an alluring field for further research. The demonstrations by Tobgy (1943) and Sherman (1946) of the mechanism by means of which reductions in chromosome number have been accomplished in *Crepis* are of fundamental importance. Additional evidence, however, is desirable and a number of similar investigations are possible, provided that the necessary artificial hybrids can be produced. Two such studies which appear to be unusually promising are those which concern the phyletic relations between each of the two other 3-paired species, *C. capillaris* and *C. Zacintha*, and its closest 4-paired relatives. In *C. capillaris* only one very close 4-paired species exists, namely, *C. parviflora*, whereas the experiments with *C. Zacintha* should include not only *C. multiflora* and *C. Dioscordis* but also *C. patula* (*cf.* Part II, pp. 742, 743).

Location of heterochromatin in Crepis chromosomes.—Heterochromatin distribution in the chromosomes of *Crepis* species, and its bearing on chromosome morphology and on changes in chromosome number through reciprocal translocations, is another almost untouched field of research. Sufficient evidence was discovered by Tobgy (1943, pp. 72-73) to show that this is indeed a very promising field.

Specific chromosome size.—The factors controlling chromosome size is another problem, the importance of which was recognized by Tobgy (*op. cit.*). In his doctor's dissertation (filed in the University of California Library) he has the following to say (pp. 129-130, 131).

If it is true that the difference in thickness between the *C. fuliginosa* and *C. neglecta* chromosomes is due to their differential synthesis of matrical chromatin, then the fact that this difference is still maintained in the parental chromosomes in the F_1 hybrid and in the second generation plants indicates that such differential activity is also autonomously controlled within the chromosomes themselves rather than by the whole genotype. The interesting observation that, in the second generation, the new chromosomes have either the *fuliginosa* or the *neglecta* thickness throughout their length, even though they had a distal segment of one arm from a parental origin different from that of the remainder of the chromosome body, suggests that the amount of the matrical chromatin in these distal segments is controlled by the centromeres or the procentric segments, either directly or through a kind of position effect (cf. Muller, 1939). The main point is, however, that chromosome thickness here is not controlled by the whole genotype but within each chromosome individually.

For the present, it must be concluded that there is nothing in the nature of a general rule with respect to disappearance or maintenance of size differences between parental chromosomes in interspecific hybrids; the outcome in a given hybrid would depend on what factors are responsible for the initial size differences in the chromosomes of the two parent species, and on whether these factors are controlled by the whole genotype or within the individual chromosomes themselves.

Tobgy's findings, then, make it obvious that much further research must be made in order to throw light on the nature of size differences between the chromosomes of related species. With the marked differences known to exist in various species of *Crepis*, this genus seems to offer especially favorable material for further research in this field.

In conclusion, the author regretfully acknowledges that "the gene contents of not a single species of *Crepis* is anywhere nearly as well explored as that of *Drosophila melanogaster*, *Zea mays*, or *Gossypium*" (Mayr, 1943), although the original purpose in attacking *Crepis* was to subject at least one species to intensive genetic analysis. Practical considerations contingent upon very limited funds for assistance, however, soon made it necessary to choose between concentration of effort upon the analysis of a single species or upon research on interspecific hybrids, which, it must be said, began, early in the history of the investigations, to offer alluring possibilities. Because of the technical difficulties involved in hybridizing and selfing, this genus can never compare with any of those mentioned above, nor with *Antirrhinum* and *Nicotiana*, in suitability for intensive genetic analysis. But these difficulties need not prevent further cytogenetic research on species and hybrids such as has been suggested above.

The other criticism of Mayr (*loc. cit.*), that "as far as taxonomy is concerned, the degree of perfection which intraspecific population analysis has reached in fishes, mammals and birds does not seem to be approached in *Crepis*," was not based on the present monograph. Nevertheless, it probably holds true in large measure. As Mayr points out, "filling this gap will require the statistical analysis of future mass collections." The need for such research is especially pronounced in analyzing such a difficult complex as *Crepis vesicaria*, *C. foetida*, *C. albida*, or *C. Di scoridis*. The statistical analysis of mass collections (in the sense of Anderson, 1941) should throw much needed light on such difficult problems, especially when these studies are supplemented by cytological observations and genetic tests of all questionable forms. Undoubtedly, a more refined and thorough population analysis offers an attractive opportunity for the modern taxonomist to place our knowledge of *Crepis* on a sounder basis.

APPENDIX 2

THE BEARING OF THE EVOLUTION OF CREPIS ON THE ORIGIN OF THE ANCESTORS OF EURASIATIC CROP PLANTS

THE CONCLUSION that *Crepis* had its origin and early development in northern Central Asia deserves consideration in attempting to establish the actual region of origin of the progenitors of the principal Eurasic crop plants. The demonstration by Vavilov (1927, 1928) that cultivated plants have five principal geographic gene centers seems to have resulted generally in the assumption that these crop plants had their complete evolution from earliest beginnings in those same centers. That such an assumption is untenable is obvious from the fact that three of these five regions (southwestern Asia, the Mediterranean region, and the highlands of Mexico, Guatemala, Colombia, and Peru) were completely submerged by the great marine transgression which occurred about the middle of the Cretaceous period (cf. Seward, 1941, fig. 106). Of the other two regions, Abyssinia was a part of Gondwana Land, and the southern part of southeastern Asia was submerged in Cretaceous times, although most of China was part of Angara Land during this period.

Abyssinia has been recognized by Vavilov as an important gene center, and it may be significant that it was part of Gondwana Land since before the Carboniferous period (Seward, 1941, fig. 49). But southwestern Asia and the Mediterranean regions were also important, and these regions were not only submerged during the Cretaceous period, when the flowering plants were strongly developing, but again in Middle Oligocene they were almost completely covered by Tethys and its connections to the northeast and southeast. Hence, the *ancestors* of the many crop plants which developed in these two regions must have had their origin and early development elsewhere.

The history of *Crepis* suggests that the ancestors of the crop plants which were developed by early man in southwestern Asia and the Mediterranean region may have migrated into those regions during Tertiary times from the Angara region. But these crop plants represent various families, and they undoubtedly have diverse histories. Some may have come from the south, for it is known that elements of the Gondwana flora migrated as far north as southern Central Asia (cf. Korovin, 1935). The possibility, however, that many of these *progenitors* of our cultivated plants were derived from the original Angara flora seems worth considering. In Cretaceous times Angara included most of China and that part of Siberia as far west as the Altai region.

The conclusion of Vavilov (1931b, p. 44; and see Huxley, 1940, p. 550) that Central Asia "cannot be regarded as the primary base of species formation," with reference to our crop plants, is based on the paucity of forms of cultivated plants in that region and on the apparent absence of well-known wild relatives along the route of the one expedition which he made. It seems fair to question whether more extensive explorations might not reveal the presence of some of those wild relatives or, if not, whether other less closely related species, representing possible ancestors of present-day crop plants, may not exist in the Altai-Tien Shan region.

But, even if northern Central Asia was not a region of origin for the ancestors of some of our crop plants, there still remains the vast region farther to the east,

where important discoveries of early angiospermous plants have recently been made (Kryshtofovitch, 1933). It seems very probable that the important crop plants of southeastern Asia had their actual origin (ancestral forms) farther north in Asia. It may be that from that same center in northeastern Asia came the progenitors of some at least of the important crop plants which were developed by early man in southeastern, southern Central, and southwestern Asia as well as in the Mediterranean region.

It is even possible that in that same Angara center there evolved the original ancestors of *Zea mays*, which has long been considered of New World origin. The recent discovery by Anderson (1943) that a certain South American variety of maize resembles certain Oriental varieties reopens the entire question of Oriental versus Occidental origin of this species.

APPENDIX 3

THE BEARING OF THE DISTRIBUTIONAL HISTORY OF CREPIS ON THE REGION OF ORIGIN OF SOME ANGIOSPERMS

IN HIS RECENT important book, *Foundations of Plant Geography*, published after the present monograph was completed, Cain (1944) emphasizes the historical aspects which are essential for an adequate understanding of present-day plant distribution. But, in the opinion of the present author, he sometimes fails to give due consideration to all the historical possibilities which should be recognized in attempting to explain such problems. For example, in his discussion of discontinuous distributions (p. 247), he refers to *Menodora* (cf. Steyermark, 1932), which is restricted to southwestern United States and Mexico, southern South America, and South Africa. According to Cain: "Steyermark finds the center of variation of the genus to be in Mexico and concludes that it had a more continuous geographical continuity at least before the end of the Cretaceous period. He believes the most logical explanation to result from the postulation of a land bridge across the south Atlantic which was obliterated by the Upper Cretaceous."

Apparently, neither Steyermark nor Cain considered the possibility of a far northern origin of the genus, followed by holarctic distribution and eventual migration into South America and Africa. The fact that *Menodora* is characteristically a xerophytic group does not lessen the probability of this hypothesis. On the contrary, the probability is actually increased, since the present geographic subgroups within the genus may logically be considered as relics of an earlier, wide distribution. It is only necessary to assume that the genus has been able to persist at all through the evolution of adaptation to xeric conditions. The same reasoning would apply to the other xerophytic genera with similar distributions which are mentioned by Cain, namely, *Hoffmannseggia*, *Fagonia*, and *Thamnosma*. This is especially clear in *Thamnosma*, in which the present-day distribution more nearly resembles that of *Crepis*, because *Thamnosma* belongs in the same subfamily of the Rutaceae as the genus *Citrus* and its close relatives, which are indigenous in eastern Asia and exist under mesophytic conditions.

The basic problem involved in explaining the widely disrupted distributions of these xerophytic groups is essentially the same as that considered by Fernald (1931) in his illuminating discussion of several other groups of plants which are now restricted to certain regions in North and South America, southern or tropical Africa, and southeastern Asia, Malaysia, or Australia. Fernald (*op. cit.*, p. 61) recognized two alternative hypotheses: Either these disrupted distributions were derived from "the widespread boreal flora of the Cretaceous and early Tertiary," or they "spread across a hypothetical trans-Atlantic land"; and he states that the former "seems to me the logical deduction." The present distribution of *Crepis*, which extends into northern Mexico, South Africa, and southeastern Asia, presents a generally similar distributional picture; and the northern Asiatic origin of this genus is clearly indicated.

APPENDIX 4

OVARY ANATOMY AS A PHYLOGENETIC CRITERION IN CREPIS

IN HIS STUDY of *Dubyaea*, the primitive endemic genus from which *Crepis* and other genera of the Crepidinae are believed to have descended, Stebbins (1940) found that the species of *Dubyaea* and of another relic, the Sino-Himalayan genus *Soroseris*, possess supernumerary vascular strands in the young ovary. He also reported that some of the most primitive species of *Crepis* have supernumerary strands of vascular tissue, whereas some of the more advanced species have the reduced vascular system of the ovary which is found most frequently in the Cichorioeae. At that time it was not feasible for the present author to make a more extensive study of ovary anatomy in *Crepis*; but more recently it has been possible to examine a number of species. These species have been selected so as to represent the most primitive and most advanced types in the genus. Furthermore, in order to determine whether there is correlation between relative phylogenetic position within the sections and presence or absence of supernumerary vascular strands, most of the species in the first nine sections were included. Using the method of bleaching reported by Stebbins (1938), it was found practicable to examine the ovaries in temporary mounts after hardening in alcohol. But in a few species having a dense ovary wall it was necessary to give a second or third exposure to hydrogen peroxide; and even then the results were not always satisfactory. This was especially notable in *C. terglouensis* and *C. alpestris*. The species examined are listed below by sections; the order within each section, indicated by Arabic numerals, is the phylogenetic order already determined on the basis of morphology and cytogenetics. Following the name of each species is given the number, in parentheses of the herbarium sheet of the University of California specimen used or the culture number of the few dried vouchers from greenhouse or garden cultures used. Lastly, is given the minimum and maximum number of supernumerary ovular vascular strands counted in the several (mostly 5-7) ovaries examined.

Section I.	1. <i>C. sibirica</i> (28.1997-5) 2-5 2. <i>C. geracioides</i> (565334) 3-6 3. <i>C. viscidula</i> (489404, 489393) 3-6 4. <i>C. paludosa</i> (74022) 0-1 4. <i>C. paludosa</i> m.v. no. 1 (442874) 1-4
Section II.	1. <i>C. kashmirica</i> (446402) 2-5
Section III.	1. <i>C. pygmaea typica</i> (656651) 2-4 1. <i>C. pygmaea anachoretica</i> (639610) 4-6
Section IV.	1. <i>C. terglouensis</i> (463914) 0-2 (ovary wall dense) 2. <i>C. rhaetica</i> (669413) 4-5 3. <i>C. Jacquinii</i> (463918) 1-3, mostly 2 4. <i>C. aurea typica</i> (669458) 0-1 4. <i>C. aurea lucida</i> (429387) 1-2 5. <i>C. chrysantha</i> (598101) 2-3 8. <i>C. albiflora</i> (565326) 0
Section V.	1. <i>C. lapsanoides</i> (194338) 5-7 8. <i>C. Mungierii</i> (429360) 0-2
Section VI.	1. <i>C. pontana</i> (669402) 4-7 2. <i>C. conysaeifolia</i> (429374) 3-5 3. <i>C. blattarioides</i> (406905) 2-4
Section VII.	1. <i>C. albida asturica</i> (31.2957-7) 2

Section VIII. 1. *C. kilimandscharica* (494389) 4-5
 3. *C. alpestris* (669456) 0-3 (ovary wall dense)
 17. *C. scaposa tarazaciformis* (565329) 4
 26. *C. Bruceae* (557860) 0

Section IX. 1. *C. tingitana* (1574) 2-3
 2. *C. leontodontoides* (259899, 669381) 0
 3. *C. suberostris* (429511) 0

Section XX. 1. *C. alpina* (463886) 0
 3. *C. rubra* (2417, 2744) 0

Section XXIV. 1. *C. nicaeensis* (31.2958-1) 0
 2. *C. capillaris* (29.2176-5) 0

Section XXVII. 3. *C. bellidifolia* (33.2940-7) 0
 7. *C. seneciooides* (30.1044-1-2-8) 0

These data make it clear that the primitive sections (I-VIII) are characterized by the presence of supernumerary vascular strands in the ovary, and that the advanced sections (XX, XXIV, XXVII) all have the reduced type of vascular system. In the intermediate or bridging group, section IX, the most primitive member has supernumeraries, whereas the other two have none. Further, in sections I, IV, V, VI, and VIII, the one least primitive species examined in each section either has a greatly reduced number of strands or lacks supernumeraries entirely, as in *C. albiflora* of section IV and *C. Bruceae* of section VIII.

Some irregularities, for example the differences in number of supernumerary strands recorded for *C. sibirica* and *C. geracioides* or for *C. Jacquinii* and *C. chrysanthia*, exist within the primitive sections I, IV, and VIII, but do not obscure the general picture. The marked difference between *C. terglouensis* and *C. rhaetica* or between *C. alpestris* and *C. scaposa* may be due to obscuration of some supernumeraries by the dense wall in two of these species. The apparently lower number in *C. aurea* as compared with *C. chrysanthia* may be an actual difference, since the former is definitely more reduced in size of the plant and its parts.

Thus, it may be concluded that a higher number of vascular strands in the ovary is positively correlated with degree of primitiveness as determined from external morphology. Furthermore, the high numbers of supernumerary strands present in the most primitive species (I—1, 2, 3; II; III; IV—2; V—1; VI—1; VIII—1) is additional evidence supporting the assumption of close relationship between *Crepis* and its putative ancestral genus, *Dubyaea*.

PLATE

PLATE 1

Fossil and present-day achenes of *Crepis*. The fossil specimens are designated by a, b, c; the others, by a', b', c'.

a, a', *Crepis terglouensis* (Hacq.) A. Kern.

a, from Reid and Reid (1916, pl. 17, no. 30).

a', from a collection of seeds received from the Botanic Garden, Innsbruck, Austria, in 1935.

b, b', *Crepis conyzaeifolia* (Gouan) Dalla Torre.

b, from Reid and Reid (1916, pl. 17, nos. 26, 27).

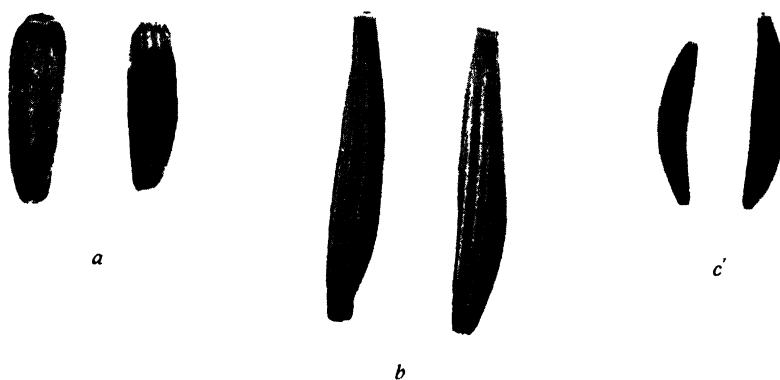
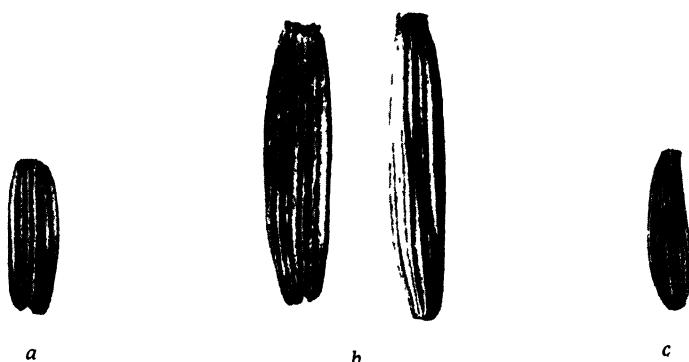
b', from Stefanoff in 1929 (UC 470082).

c, c', *Crepis mollis* (Jacq.) Asch.

c, from Reid and Reid (1908, pl. 13, no. 96).

c', left, from Herb. Willd. (B) n. 14680-1.

right, from hort. genet. Calif. 28.2201-12 (UC 531725).



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